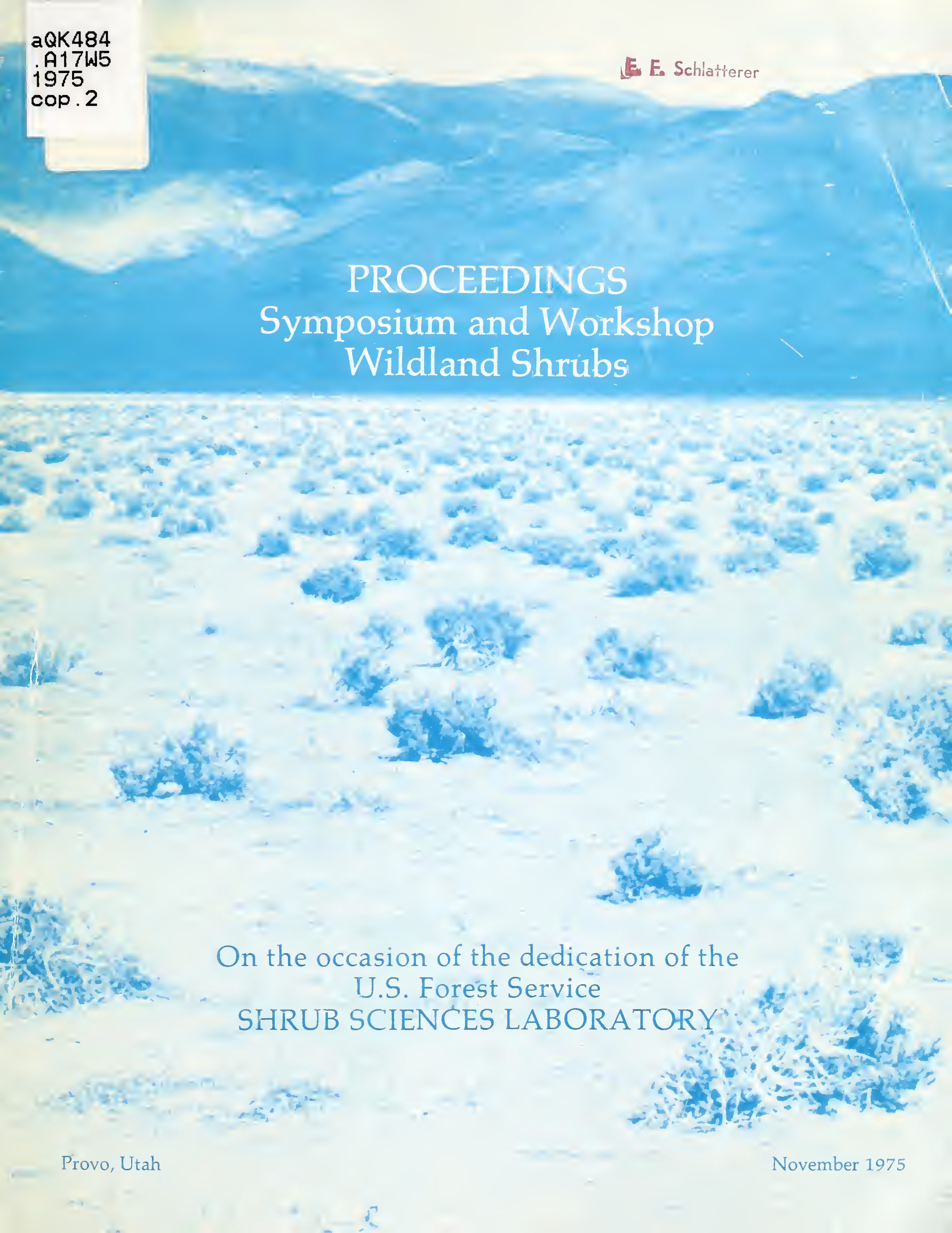

PROCEEDINGS
Symposium and Workshop
Wildland Shrubs

On the occasion of the dedication of the
U.S. Forest Service
SHRUB SCIENCES LABORATORY

Provo, Utah

November 1975

Wildland Shrubs

Symposium and Workshop

Proceedings

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Shrub Sciences Laboratory

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WILDLAND SHRUBS

Symposium and Workshop

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Sponsored by

Intermountain Forest and Range Experiment Station,
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Utah Division of Wildlife Resources
Brigham Young University
Utah State University
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FOREWORD

It would be difficult to imagine a more exciting time than right now to be involved in shrub research. Although appallingly little is known about the genetics, physiology, evolution or ecology of shrubs, tooled as we are with techniques and knowledge derived from experience with cultivated crops and range grasses, we can look ahead with confidence to a golden era of profitable shrub research. Not only are shrubs intriguing as a peculiar life form whose adaptive strategies have made them uniquely successful throughout nearly one sixth of the exposed land surface of the earth, but they also comprise the single most valuable natural resource throughout much of Australia, Africa, Eurasia and western North and South America. On millions of acres their economic and aesthetic contributions are unmatched.

It would also be difficult to select a more favorable site for the center of shrub research than Provo, Utah, where the new Shrub Sciences Laboratory has been constructed. Provo is centrally located in the world's most extensive stand of big sagebrush (*Artemesia*). It sits at the juncture of the vast warm deserts of the south and the cooler deserts to the north. Mountain brush covers the foothills of all surrounding mountains. Extensive saline deserts, dominated almost solely by shrubs, cover millions of acres of Nevada and California on the west, Wyoming, Montana and Idaho on the north, Eastern Utah and Western Colorado on the east, and New Mexico, Arizona and Old Mexico on the south.

Provo's climate is also nearly ideal for shrub studies, being a pleasant compromise of the extremes which characterize contiguous areas. It is uniquely on the boundaries of three great physiographic provinces: the Rocky Mountain Province to the east, the Great Basin Province to the west and the Colorado Plateau to the south. Because of its particular setting, astride north-south as well as east-west migration lanes, nearly every important wildland shrub of the Intermountain West is present or nearby.

Although only a relatively few scientists are currently engaged in shrub research, nearly every facet is being covered by those stationed at the Provo Shrub Sciences Laboratory or in nearby stations and institutions. Frontier studies are already well underway in shrub genetics, taxonomy, ecology, pathology, entomology, physiology, cytology and evolution. Experiments have been initiated to improve seed germinability, seedling establishment, shrubland management and extended shrub utilization. Shrubs offer new extensive opportunities for landscaping, rehabilitation of disturbed areas, pollution control, and watershed management. Because of their demonstrated widespread accomodation and multiple uses in nature, the upcoming years are predictably the "day of the shrubs." The only possible limitations lie within our own dedication and imagination.

INTRODUCTION

In conjunction with the dedication of the U.S. Forest Service Shrub Sciences Laboratory, held November 6, 1976, at Provo, Utah, a workshop and symposium was organized to provide a survey of the most important facets of shrub research currently underway in the United States. A session was also organized for contributed papers solicited from scientists actively engaged in shrub research. The workshop was held on Tuesday, November 4, 1976, with James P. Blaisdell as moderator. Participants presented oral reports, summarizing current research activities in the various laboratories. A list of those present and a short summary statement of the presentations have already been circulated by Dr. Blaisdell so are not included in these proceedings.

Twenty-two contributed papers were presented on Wednesday, November 6, 1976, with Cyress M. McKell as moderator. Abstracts of each of these papers are included in this publication. They are arranged in the sequence in which they were given except for minor shifts to place together similar subject matter.

Four major topics were selected by the steering committee as representing some of the more exciting frontiers of shrub research. Selected participants presented these topics at the symposium held Thursday morning, November 7, 1976. The symposium was moderated by Howard C. Stutz with G. Ledyard Stebbins, Joseph E. Goodin, Raymond B. Farnsworth and Stephen B. Monsen as the invited participants. Monsen's

paper was coauthored by Donald R. Christensen. These papers are presented in full in these proceedings.

The dedication of the Shrub Sciences Laboratory was held Thursday afternoon under the direction of Roger R. Bay. An outline of the dedicatory services is provided on page 112.

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Section I -- Symposium

SALINITY RELATIONS IN SHRUBS

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The vegetation of saline shrublands represents a unique kind of biology from the standpoint of evolutionary adaptations that have led to the ability to compete in what man considers to be one of the harshest environments the earth has to offer. I would propose that the concept of a harsh environment is in the eye of the beholder, and that the physiological adaptations which give a selective advantage to shrubs occupying saline habitats, although unique, represent no more of a hazard to survival than do the flora occupying mesic sites.

Not all saline sites have been that way since the beginning of time. One can look, for example at the Great Basin and its rather extensive saline deposits, most notably the Great Salt Lake area. Salt of inland continental areas is derived from several sources (Chapman, 1966):

(1) Marine sedimentary deposits laid down in Jurassic, Cretaceous, or Tertiary periods

(2) Saline deposits associated with a former arm of the sea which, as a result of land or sea level changes, is no longer inundated

(3) Salt blown inland from the sea over long periods of time and deposited (aeolian salt), as for example in

South West Africa

(4) Inland lake basins in which the natural drainage outlet ceases to exist, and subsequent drying of the former lake brings about a concentration of salt that has accumulated in the waters. The best example is the Great Salt Lake, a remnant of Lake Bonneville, a much larger Pleistocene lake which formerly occupied the eastern part of the Great Basin. Evidence of this ancient lake is readily observed as a series of terraces on the lower slopes of the surrounding mountains. The lake rose to about 1,000 feet above the present level, and at that time it had a long history of constant level. Its maximum dimensions were some 346 miles long and 145 miles wide. It occupied a large part of western Utah and extended slightly into eastern Nevada and southern Idaho (Flowers and Evans, 1966). Glacial conditions existed at that time, and an increase in precipitation caused the lake level to rise, finally overflowing at a low point near the northern end of the lake at Red Rock Pass, Idaho. This point acted as a highly-erodable spillway, which cut a canyon to a depth of some 375 feet in only 25 years. The area of the lake was reduced by 1/3 in a short time, and finally stabilized until climatic changes led to a drier climate and an accelerated rate of evaporation. When the level reached about 200 feet above the present level, salt had concentrated to a considerable

extent, and began to be deposited in the sediments. The decline in the lake took some 15,000-30,000 years eventually dividing into several small lakes, and the Great Salt Lake is the only one of consequence which remains.

Because of the varied nature of the origin, the deposits may be near the surface or some distance below it. There are two major soil types that present salinity problems (Chapman, 1966):

(a) Solonetz - characterized by a definite structure and profile. Sodium is present as carbonate, with or without sulphate and chloride. The water table is fairly deep and accumulation of salt is also at some depth.

(b) Solontchak - characterized by little structure; sodium is usually present as chloride, with or without sulphate and carbonate. Salt accumulates in surface layers, and unless there is irrigation or substantial rainfall surface salt is likely concentrated enough to prevent plant growth.

Salinity effectiveness varies with a whole series of factors including precipitation which determines the degree of leaching, depth to salt accumulation, and need for irrigation. The proximity to drainage channels will determine localized salt concentrations, and closed basins lead to salt transport and extreme concentration. The nature of the soil is important--heavy soils tend to

accumulate and hold excess Na^+ and Mg^{++}. It is also more difficult to remove excess alkali from such soils. A dense vegetation cover may reduce evaporation from the soil, but transpiration demand may tend to move deep salts closer to the surface. As vegetation cover decreases, surface evaporation increases and may leave crystalline deposits on the surface. Slope determines the drainage pattern and soil will be more saline towards lower levels. The nearer the water table is to the surface, the more constant will be the salinity. Water flow into a region usually comes from higher altitudes, and is therefore generally lower in salinity. Even so, total influx may not exceed total transpiration, and salinity gradually increases. High summer temperatures accelerate rates of evaporation and tend to bring about excessive summer salinities.

In view of these parameters of precipitation pattern, geologic history, temperature, etc. it is not surprising that a large portion of our western arid and semi-arid rangelands can be considered at least moderately saline. Salinity follows a mosaic pattern, and localized areas may be exceedingly saline, whereas a relatively non-saline condition exists only a few meters away.

The distribution of plant species over the surface of the earth is controlled by a complex of climatic and edaphic factors. Certain plant species are found more abundantly

on soils with certain chemical properties than on other soils. The western range, in many respects similar to other rangelands of the world (McKell and Goodin, 1973; Moore, 1973), is characterized by its extremes of temperature, precipitation, and soils. Moisture is probably the most important formative factor in determination of vegetation type, particularly in arid and semi-arid regions, but the chemical constituents of the soil determine to a very great extent the vegetational parameters. Because of the osmotic effects imposed by high concentrations of soluble salts in the soil solution (leading to a very negative solute potential), salts and precipitation interact to give a complex mosaic of vegetation patterns far more complicated than that suggested by total precipitation. The species which are able to tolerate excess salts run the gamut of susceptibility, and many plant lists have been developed which represent salt-sensitive, salt-tolerant, and intermediate species (Richards et al., 1954; Waisel, 1972). But the molecular basis of salt tolerance, although poorly understood, suggests that each biotype has a particular set of biochemical factors which leads to that tolerance. Thus, classification of species based on tolerance is at best only an approximation. Shreve (1942), for example, classified halophytes around the Salt Lake basin according to relative salt sensitivity:

(a) 2.5% salt in the soil (_Salicornia_ spp. and _Allenrolfea occidentalis_)

(b) 0.5 to 0.9% salt (*Distichlis spicata* and *Sporobolus airoides*)

(c) 0.8% salt (*Sarcobatus* spp., *Atriplex confertifolia*, and *Kochia* spp.)

(d) 0.4% salt (*Artemisia tridentata*)

In typical salt lakes or depressions, saline soil solutions limit the vegetation such that one may find only halophytes from the higher plants which have "out-competed" the less tolerant vegetation. Some genera, like *Spartina*, excrete salt through special glands. Others, like *Salicornia*, *Allenrolfea*, and *Saueda* apparently compensate for excess salt by the uptake of water that is stored in succulent tissues. Sometimes the concentration of salt, even in succulent tissues, may become lethal and the senescent tissues or organs are simply sloughed off (Chapman, 1966). Probably the most economically-important genus of rangeland halophytes is *Atriplex*. Many species in this genus manage to cope with excess salinity by storing Na^+, balanced by the synthesis of oxalate anion (or more rarely by Cl^-), in vesiculated hairs (trichomes) on the leaf surfaces (Osmond, 1963; Osmond, 1967). Whenever the concentration of salt reaches some lethal level, the balloon-like cell bursts, leaving a litter of cell wall debris and salt crystals on the leaf surface (Mozafar and Goodin, 1970). This natural

mulch is thought to reduce the transpirational losses from such plants by providing a barrier of increased resistance to the vapor pressure gradient.

In those regions of the world where precipitation is sufficient to contribute to considerable biomass production, relatively pure rainwater moving through the soil apparently assures the plants living there of a temporary reprieve from their so-called hostile environment. The dilution effect, even in very saline lakes, may be of sufficient magnitude and duration to allow for temporary flushes of growth--perhaps a revitalization for an otherwise weakened plant. There can be no doubt that such a mechanism accounts for that chance for certain seeds to germinate. We often see that even in halophytes, seed germination and early seedling growth is greatly inhibited by low concentrations of salt; yet the established plant may be exceedingly resistant to salt.

The water cycle establishes a continuum for uniting the oceans, rivers, streams, and the soil through which it permeates. Most of the earth's surface is covered by water, and it might appear to the casual observer that all of our water needs could be met for the forseeable future (Hunt and Garrels, 1972). But most of this water is salty, practically all of it residing in the oceans at any given time (Goodin and Mozafar, 1972).

Vegetation distribution is dictated more by the distribution of fresh water than any other single environmental factor. Even the influence of temperature is mediated by the relative amount of water in the soil and atmosphere. Where rainfall is abundant and evenly distributed, lush vegetation results as, for example, in a tropical rain forest. But as precipitation becomes limiting, even for a short portion of the growing season, forests are replaced by grasslands and further decreases result in semi-arid and finally arid deserts with their sparce vegetation and low biomass production (Kramer, 1969). As an example of development of a biome, the North American grasslands have developed east of the Rocky Mountains, from northern Mexico on the south to Saskatchewan on the north, and eastward in the shape of a wedge to Indiana and Ohio. Climatic changes, brought about primarily through the uplift of the Rocky Mountain system, are thought to be responsible for the development of the North American prairies. Winds blowing moisture-laden clouds from the Pacific dropped much of their moisture on the west side of the mountains, and winds blowing eastward became drier and great areas of low summer rainfall and dry winters resulted (Wilsie, 1962).

Where potential loss of water from evaporation and transpiration exceeds the annual precipitation, dry climates and their associated sparse vegetation results. In such

a climate, variability in precipitation is unusually high, as is the risk to vegetation stability. Boundaries of dry climates are difficult to define, and a more meaningful approach to the problem is a consideration of effective precipitation, in which one considers not only total precipitation, but the rate at which it falls and the rate of evapo-transpiration. The distribution of precipitation in dry regions may be quite sporadic, with a few heavy downpours accompanied by a high percentage of runoff. This concept of effective precipitation has been elegantly explored by Thornthwaite (1948).

Most ecologists distinguish between arid and semi-arid vegetation and climates. Although the boundary is arbitrary, one might consider a 20-inch precipitation zone as the upper limit for a true arid climate (Trewartha, 1954). Dry climates are extensive, particularly at 30 degrees north and south latitudes, and occupy about 26% of the continental land area of the world.

The secret of the ocean is the ability of water to soak up heat without much temperature change (Hunt and Garrels, 1972). Circulation within the ocean allows for water being warmed in certain parts of the world to move to the colder portions of the ocean. The greater the heating, the more rapid the circulation. When sea water evaporates, the salts are left behind and the fresh

water vapor moves into the atmosphere. As the vapor rises, it cools, condenses, and finally rains back on the sea. If there were no land masses, the system would be quite simple. But there is a time lag between evaporation and rain return, and the evaporated moisture may travel long distances in the atmosphere before it condenses and falls as rain, snow, or ice on the land or ocean. If the precipitation does fall on land, it may evaporate again, or collect on the surface, percolate into the soil, or run off across the surface eventually flowing back into the sea.

On the average, some 27 inches of precipitation falls on the land masses of the world each year; the figure is slightly higher for the amount of precipitation which falls back directly into the ocean. About 2/3 of the terrestrial precipitation evaporates into the atmosphere and comes back to the sea as rain, and about 1/3 returns to the oceans by streams and rivers. If we could contain all the water that falls on the earth, there would be approximately 40 million gallons of water per year for every person on earth. The problem is one of collection and distribution (Hunt and Garrels, 1972).

The water cycle is driven by energy from the sun, and about 1/2 of the sun's total energy received at the earth's surface goes toward heating the water given off in evaporation.

Most of the water returned to the atmosphere is not given back directly as evaporation from the soil surface, but as evapotranspiration from plant surfaces. Thus, in man's transportation of water from place to place on the earth's surface, little of that water is "used", but it is merely recycled. The water cycle is one of influx, storage, and eflux. Therefore, it is possible to quantify the water budget at any point in time.

Historically, water distribution on the land masses has determined the migration to and colonization of various parts of the world. Early development of communities and villages occurred because of access to a predictable water supply, and even today the location of urban development and industry is dictated by water supply. With the advent of modern technology, localized access has become less important and now we find grandiose schemes for the movement of large quantities of water from one region to another, sometimes over distances of hundreds of miles.

At least 1/3 of the earth's surface is arid or semi-arid; much of its soil and water is too saline or alkaline for traditional agricultural production. Not all of these regions have always been salty; in some areas, natural surface flow of water carries dissolved salts to previously nonsaline soils. Ground water dissolves various

substances from the soil and porous rock, including sulfuric acid from high sulfate clay, and calcium bicarbonate from reactions with limestone. Other substances, such as magnesium, sodium, potassium, iron, manganese, phosphorus, and silicon are found in the rocks as carbonates, sulfates, nitrates, chlorides, bromides, fluorides, and iodides (Overman, 1968). In arid lands, these geologic salt deposits are eroded; as a result, dissolved salts are spread over large areas. High rates of evaporation and low rates of leaching concentrate the salt in the upper soil and surface waters more rapidly than in regions of higher precipitation.

Elaborate irrigation schemes throughout the world have contributed significantly to this relocation of salt. As supplies of high quality water dwindle, the concentrating of salts is accelerated, requiring larger quantities and more frequent "flushing" of the soil in order to leach out excessive soluble salts. Most agricultural crops cannot tolerate high quantities of salts in the soil. Poor quality of both surface and ground waters is a limiting factor in the success of irrigation in many areas (Richards, 1954).

Many plants are capable of cycling salts through the soil-plant system, and persistence of such plants is essential to the functioning of the ecosystem. Critically

important plant nutrients, such as nitrates, occur as so-called "islands of fertility" in arid regions (Garcia-Moya and McKell, 1970). These pockets of concentrated nutrients are essential to the delicate balance of arid ecosystems, and any displacement of a species component will probably result in the loss of a particular nutrient through leaching. Once it is gone, there is little chance that nutrient input will coincide with establishment of a new plant (either the same or another species) to fill the niche.

Salt stresses may occur from both desirable and undesirable salts, and one of the most common examples of salt stress occurs with excessive fertilization. High concentrations of soluble salts in the root medium affect plant growth in several ways. The total water potential at the root surface may be lowered, primarily as a result of a very negative solute potential, causing absorption of water by the roots to be inhibited. Specific ions in the saline media may induce toxicities or deficiencies of one or more of the mineral elements in the plant. And in some cases, there may be a combination of osmotic and specific ion effects (Hayward, 1957). The problem of how soil salinity affects plant uptake and utilization of essential mineral elements can be extremely complex. Examples are sulfate-induced calcium deficiency and

calcium-induced potassium deficiency (Bernstein and Hayward, 1958).

The general consequence of increasing the concentration of salts in the soil solution is one of growth suppression more or less proportional to the solute concentration, but the degree of suppression varies from genotype to genotype. The effect of salinity on yield of marketable products may not necessarily be influenced to the same degree as total physiological yield (Slatyer, 1967). In vegetables, for example, the product is often measured in fresh weight, and a salt-imposed reduction in dry weight may be compensated for by an increase in succulence. This is particularly true of species which are salt-tolerant (Magistad et al., 1943).

Thermodynamic considerations suggest that a solute potential imposed by salts leads to a water potential identical to that imposed by a negative matric potential, or lack of water in the soil. Indeed, a combination of matric, solute, and pressure potential are summed to arrive at water potential for any part of a system (Brown and Van Haveren, 1972). However, it is apparent that if significant uptake of the salts do occur (i.e., osmotic adjustment) and if the plant behaves in any manner <u>other</u> than a perfect osmometer, then the ultimate effect on plant growth and development may be very different, depending

upon whether the stress was imposed by drying of the soil or a salt-imposed physiological drought. Bernstein (1961) and Slatyer (1961) confirm that there is effective osmotic adjustment in both roots and shoots to imposed osmotic substrates.

The presence of electrolytes in the root medium generally results in much enhanced concentrations of electrolytes in the plant, with adverse effects on the ion balance within cells and tissues. The composition of the electrolytes absorbed may broadly reflect that of the substrate, but tolerance to salinity appears to require a high degree of ion selectivity. Salt tolerance of various agricultural crops is apparently related to regulation of ion uptake (Van den Berg, 1952). As with normal salt uptake, the primary discriminatory barrier appears to be in the root, so that xylem sap concentration of chloride ions may be very low, even though accumulation may proceed in individual cells in the shoot (Scholander et al., 1962).

Kessler et al. (1964) reported that salinity strongly suppressed RNA and DNA accumulation, particularly in the initial stages of salinization. So-called "salt respiration" suggests an increased synthesis and/or activity in response to high concentrations of salt.

The progressive reductions in growth rate caused

by increasing salinity appear to be caused primarily by the effect of excess ion accumulation in affected plants. Direct osmotic effects, acting through reduced water availability to the plants, appear to be of secondary importance, except as initial responses to the imposition of saline substrates. These differences, between soil water stress mediated by water availability and internal water deficits, and salinity stress mediated by excess ion accumulation, are illustrated by experiments dealing with plant response to stress removal. On removal of soil water stress relative growth rates more rapid than those in control plants are frequently observed (Gates, 1955a, 1955b). Relative growth rates following salinity treatments are less rapid than in the control (Greenway, 1962). This is probably not only a result of different forms of metabolic inhibition during stress, but to the length of time required, following salinity treatments, for the excess ion accumulation within the plant to be diluted by new growth (Slatyer, 1967).

The tolerance of plants to chloride and sodium ions may be associated with the relatively low rate of ion absorption (Greenway, 1962). Salts in large quantities in the plant cells have direct or indirect effects on protein hydration (Klotz, 1958). This may lead to the

enhanced succulence observed under saline conditions in some species (Nieman, 1962).

Changes have been reported in protein conformation and enzyme activities at low concentrations of sucrose or NaCl (Slatyer, 1967). Similar effects may be induced by isosmotic substrates of different compositions (Gauch and Wadleigh, 1944). These interactions take place at molecular levels, and therefore different results may be expected; e.g., K^+ ions, which do not disturb the icelike structure of the hydration water of proteins, and Na^+ ions, which do disturb it (Kavanau, 1964). An excess accumulation of electrolytes in plant cells, especially of ions such as Na^+ and Cl^-, can be expected to result in progressive changes in protein hydration and in enzyme activity (Slatyer, 1967).

Plants grown on saline media may regulate their ion uptake to a certain extent, but generally an increase in salinity causes an increase in ion uptake an a consequent buildup of salts in the plant. The excessive uptake of cations by plant cells in commonly associated with an increase in the synthesis of organic acids (Jacobson and Ordin, 1954; Osmond, 1963). Sometimes the organic acid produced may not be favorable as far as food or forage value of the crop is concerned (Goodin and Mozafar, 1972). Livestock intoxication by

Halogeton glomeratus is attributed to this plant's excessive synthesis and accumulation of oxalic acid in response to excessive uptake of Na^+ ions (Williams, 1960).

Many different salts at equivalent osmotic potentials often produce equivalent growth depression (Hayward and Long, 1941). Reduction in growth under saline conditions apparently occurs as a result of a very negative solute potential in the soil solution which causes the overall water potential to also be quite negative, thus resulting in a decrease in the water uptake by the plant (Hayward and Spurr, 1944). Physiological drought caused by osmotic inhibition is sometimes difficult to distinguish from drought caused by a lack of water in the soil; in the latter case, the negative water potential in the soil is brought about by a negative matric potential. The interactions of salinity and drought are complex. The theory of osmotic inhibition has been challenged by investigators who point out that plant cells maintain internal osmotic pressures (negative osmotic potentials) sufficiently higher than that of the external medium to effect an adjustment that prevents osmotic loss of water to the medium (Bernstein, 1961).

The total volume of water absorbed by a plant is

affected not only by the rate of absorption, but also by the water-absorbing area of the root. Plants with shallow root systems or with large top-to-root ratios show a reduced capacity for water absorption, and thus have poorer salt tolerance than plants with deep roots or those with low top-to-root ratios (Bernstein and Hayward, 1958). A decrease in top-to-root ratio has been observed with increases in salinity (Bernstein and Pearson, 1954). If osmotic adjustment occurs, the plant's absorbing capacity should not be impaired by the decrease, but osmotic adjustment does not always occur (Mozafar and Goodin, 1970).

An element present in the soil in excess may cause metabolic disorders. It competes for entry with other elements present at lesser concentrations, and once absorbed, may inhibit enzymes, displace other essential elements from their normal, functional sites, precipitate other essential elements, disrupt the structure of water, and otherwise disturb plant metabolism (Epstein, 1969). Actual concentrations need not be very high to produce some of these effects.

Although the effects of salinity on specific metabolic reactions have long been postulated, experimental data are scanty. In alfalfa and tomatoes, Kling (1954) noted that growth inhibition due to increase in salinity

was accompanied by an increase in succulence and the production of darker green leaves. Boyer (1965) found a slow decline in net photosynthesis in cotton with increasing salinity. The stomata were reported to be open, and therefore the effect was attributed directly to salinity. There are many reports that increasing salinity increases rates of respiration (Nieman, 1962) and therefore specific enzyme systems associated with respiratory metabolism can be assumed to increase in activity. Such an increase would directly suppress growth by increasing net assimilation rate (Slatyer, 1967).

Very few ionic species in soil solution or absorbed on the soil particles contribute to salinity in a given saline soil. The predominant cations and anions in soils are Ca^{++}, Na^{+}, Mg^{++}, Cl^{-}, $SO_4^{=}$, HCO_3^{-}, and $CO_3^{=}$. Saline soils contain Na^{+}, Ca^{++}, and Mg^{++}, but of these cations, Na^{+} cannot exceed a given concentration if deterioration of soil structure is to be avoided (Richards, 1954). High concentrations of Mg^{++}, for example, can be harmful to the plant, not only because they are toxic to the plant tissue, but also because they can greatly reduce the absorption of Ca^{++} and K^{+} (Hayward and Wadleigh, 1949). If relatively high concentrations of Ca^{++} accompany the Mg^{++}, this effect is usually

avoided. High concentrations of Ca^{++} can produce a nutritional imbalance, however, unless accompanied by some other cations such as Na^{+} or K^{+}. Van den Berg (1952) has suggested that salt tolerance is related inversely to the degree of calcium accumulation by the plant.

The specific ions likely to be most abundant and to cause the greatest problems are Na^{+} and Cl^{-}. Plant response to excess sodium may be complicated by indirect effects, such as structural deterioration of sodic soil with consequent poor growth of the plant because of restricted moisture transmission and seedling emergence. Direct effects of Na^{+} are its toxicity to sodium-sensitive crops and the change it imposes on the balance of nutrients in the relatively tolerant plants (Mozafar, 1969).

Selective ion transport is all important in the salt economy of all plants, including halophytes (Epstein, 1969). It allows the plant to selectively absorb from the soil solution essential nutrients in amounts conducive to growth and function; it regulates the flux of ions present in the external medium at high concentrations; and it helps to maintain internal osmotic pressures higher than those of the surroundings, and consequently, to allow water to continue to be absorbed. Even though most crop plants cannot tolerate salt concentrations

exceeding a few hundred parts per million, many halophytes can cope with concentrations up to and exceeding that of sea water (Rains and Epstein, 1967).

Biological membranes can transport ions against concentration gradients and electrical potential gradients. The necessary energy for this transport is believed to be furnished by metabolism (Epstein, 1965). Ion transport across these membranes for long periods of time can result in a much greater concentration of ions within the cells than in the solution bathing the cells (Sutcliffe, 1962). A proposed mechanism of selective ion transport across a membrane which is impermeable to free ions is the "carrier concept" (Epstein and Hagen, 1951).

Levitt (1956) defines resistance to an environmental factor as the ability of an organism to prevent that factor from invading it, or tolerance of such a factor when it does invade the organism. It is also the ability to survive full impact of the unfavorable environment without any protective barrier.

The fact that only a small group of higher plants can grow under saline conditions was recognized many years ago. But salinity is not incompatible with plant growth and development (Rains, 1972). It is simply a matter of degree and the relative sensitivity of specific

plants. Great variations exist regarding responses to salinity. Certain bacteria are very salt sensitive; others are listed among organisms with the greatest tolerance. Some of them (e.g., Halobacterium) survive in the Dead Sea (Waisel, 1972). On the other hand, fungi, mosses, ferns, and gymnosperms are usually quite sensitive and are not found in saline substrates.

Various adaptive mechanisms have been selected in halophytes in the course of evolution. Some organisms are evaders, restricting their life cycle to those seasons when the substrate is most dilute. Others exclude salt, whereas another group may cope with the salt by tolerating it within its tissues, or excreting it through a salt gland, vesiculated hair, etc. (Mozafar and Goodin, 1970).

Considerable evidence for many different kinds of plant materials now suggests that cation absorption occurs by a dual absorption mechanism, the first occurring at a concentration below 1mM, and the second occurring at a concentration between 1 and 50 mM. Mechanism 1 shows higher specificity for K^+ than does Mechanism 2. The uptake kinetics of this system is only operative in the presence of Ca^{++} (Epstein, 1969; Rains, 1972).

There are two features of a saline environment with which cellular transport mechanisms must cope if essential

nutrients are to be acquired in physiological quantities. First, even in saline substrates the concentration of some macronutrients may be low. The absorption mechanism must be able to absorb and build up ions against a concentration gradient. Second, such an environment contains other ions at high concentrations which are potential competitors of the essential ions. The transport mechanism must therefore possess a high degree of specificity for essential ions.

Potassium, for example, is the mineral nutrient cation needed by plants in the largest amount. Yet in soil solution its concentration rarely exceeds 1 mM (40 ppm). From these dilute solutions the roots of growing plants must absorb K^+ essential for growth. In this case, only mechanism 1 has sufficient affinity for potassium to allow for absorption at rates sufficient for plant metabolism. Even at concentrations at 0.02 mM, absorption occurs at one-half the maximal rate of mechanism 1. At this concentration, mechanism 2 is inoperative (Epstein, 1969). Even in the presence of a very high concentration of competing ions, such as Na^+, the mechanism 1 for K^+ absorption shows a great deal of resistance to competition by Na^+. This specificity for the type 1 mechanism is found in both salt-sensitive and salt-tolerant species.

The term halophyte refers to those plants which are able to somehow cope with high concentrations of salinity, generally Na^+. Since halophytes are able to thrive at high salt concentrations, one would expect the characteristics of mechanism 2 to be an important factor in the salt economy of halophytes. For example, in tall wheat grass, a salt-tolerant species, mechanism 2 absorption of chloride and alkali contributes much more to the total rate of absorption than is the case in intermediate wheat grass, a relatively salt-sensitive species. In other halophytes, including mangrove (*Avicennia marina* Forst), absorption of potassium at high concentrations occurs by mechanism 2.

Many of the *Atriplex* species apparently accumulate alkali cations via mechanism 2. *Atriplex vesicaria* will grow in nutrient solutions containing 1 M NaCl (twice the concentration of sea water). Black (1960) found two absorption mechanisms, one highly selective for potassium and the second functioning at high concentrations of either Na^+ or K^+.

The demands imposed on natural resources by population and energy pressures have caused a reassessment of our rangelands. Regions heretofore considered too dry or too salty have suddenly become an integral part of the resource. Most range managers have emphasized the

importance of grass, and any range too poor to grow grass was considered too poor for production. Certain salty lakes which grow salt-tolerant grasses have been utilized for livestock grazing during the early stages of plant development, but these usually become unpalatable late in the season. Other managers have long recognized the importance of certain halophytic shrubs, as an important feed for domestic livestock and wildlife. *Atriplex* is recognized throughout the western rangelands as an important high-protein, winter feed. There has been a long-standing interest in certain species of *Atriplex* as a forage shrub, and recent attempts have been made to intensify its cultivation (Goodin and McKell, 1970). Cutting *Atriplex* forage as a hay crop was found to be feasible and yields exceeding 16,000 kg/ha/year were recorded, and the results suggested that such plants have considerable potential in marginal lands subjected to prolonged drought and excessive salinity.

Not all halophyte species are so desirable. *Halogeton glomeratus*, for example, is a recent weedy invader of western rangelands and has proven to be a fierce competitor. Unfortunately, it accumulates large quantities of oxalic acid which often results in the death of livestock.

The range managers of the world have finally come to the realization that wildland shrubs make an important contribution to total productivity in the rangeland ecosystem. With proper management of saline shrublands, we will discover that many regions of the world neglected as a renewable natural resource have the potential of adding substantially to world productivity.

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NITROGEN FIXATION IN SHRUBS

by

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R. B. F. 1/21/76

NITROGEN FIXATION IN SHRUBS[1]

by

Raymond B. Farnsworth[2]

This Symposium and dedication of the new Shrub Sciences Laboratory of the U.S.D.A. Forest Service is a most significant and fitting occasion as a part of the Centennial year at Brigham Young University. It is good to participate with you at this time.

I have been invited to talk with you today of the subject of nitrogen fixation in shrubs. Particularly about that group of plants now referred to as the nodulated non-legumes.

This is an area in which little information actually exists. There is really a dearth of information on this subject and it is an area of research which I hope would receive a lot of attention in the future of this new Shrub Sciences Laboratory.

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[2] Professor of Agronomy, Brigham Young University.

The threat of food shortages throughout the world is becoming more and more apparent. The problem becomes even more acute as one realizes that protein deficiency is rapidly becoming one of the major problems of mankind. This becomes even more evident as the population explosion continues.

We know that about 95% of all of the nitrogen supply of this world is locked in the bank called the atmosphere. It is one of the essential elements in the composition of protein and yet it is not readily available in quantities sufficient to relieve the shortage of protein.

The ability of man to solve this riddle of nature and in helping to work out some of the answers to the question of nitrogen fixation will be the means of making more nitrogen available for the formation of plant and animal protein.

Actually, most of the information regarding nitrogen fixation has been known for less than 100 years. Presently there are too few involved in research on this very important problem.

There is considerable work being done throughout the world on nitrogen fixation and many of the investigations are associated with the mechanism and biochemistry of the process. Most of the researchers on this project are not involved with different kinds of plants and plant systems which might be associated with nitrogen fixation. The number of those of us in the United States who have been associated with nitrogen fixation among the non-legumes, and particularly on the shrub plants can be counted almost on the fingers of two hands.

Let me attempt to give you an idea of just how few people in the United States are investigating plants and plant systems which may be nitrogen fixers.

Dr. Youngberg of Oregon State University has probably done more work on *Ceanothus* sp. (deerbrush, or snowberry) than any. Considerable work has

also been done by Delwiche, Hellmers, Vlamis and their associates in California. Dr. Art Wallace and Dr. Evan Romney of U.C.L.A. are involved in studies of nitrogen fixation of desert shrubs at the Nevada Test site of the A.E.C.

Soon after I discovered nodulation of Artemisia ludoviciana, Dr. Romney and I discussed this possibility of nitrogen fixation and he and Dr. Wallace began to look more carefully for probably nitrogen fixers in that area. They report having observed nodulation of Artemisia tridentata, and acetylene reduction by Kramaria sp. and several other plants in the Test site.

There is also Dr. Porter at Colorado State University; Dr. Zak at Massachusetts State and Dr. Fessenden now at Quebec who are working with the Myricaceae, Dr. Wollum at North Carolina, Dr. Staffeldt at New Mexico, and Dr. Gilmour and his son at Arkansas. Dr. Gilmour and Dr. Wollum had worked previously with Dr. Youngberg at Oregon State.

A considerable amount of research has been done in the past and is still being pursued on Alder, Alnus sp. of the Betulaceae by Daly, Goldman, Frederick, Thornton, Zavitkovski and Newton.

At Florida, Shank in association with Dobereiner and others of South America are working on the probable nitrogen fixation of grasses, corn and sugar cane. Wullstein while at the University of Utah, was working with Indian rice grass.

Some of the biochemists currently involved in the process of nitrogen fixation are Dr. Hardy of E.I. du Pont de Nemours and Company, Dr. Burris of Wisconsin, Dr. Strobel of Montana, Dr. Evans at Oregon State and their associates.

These names have been given **only** to indicate how small the number is of scientists in the United States involved in this critical problem, and to particularly point out that not many are involved in nitrogen fixation by the shrubs.

The observation of nodulation of plant roots is not new. Fuchs is recognized as having observed and diagramed nodules on the roots of four species of legumes in 1542 (Fred et al, 1932). In the early observations nodules were referred to as

"swellings on the roots of plants caused by insect larvae." These swellings or galls were also reported on the leaves and aerial portions of many plants.

Malpighi is recognized by some as the first to report nodulation. In 1679 he reported nodulation and said that they were galls caused by an insect. In another paper in 1687 he still referred to the swellings as galls caused by an insect (Burrill and Hansen, 1917; Waksman, 1927, Fred et al, 1932).

It was not until 200 years later, in 1884-1886, that Hellriegel, Wilfarth and Atwater (Waksman, 1927) demonstrated that nodules on the roots of legume plants were actually effective in the process of nitrogen fixation.

In 1888 Beijerinck (Burrill and Hansen, 1917; Waksman, 1927; Fred et al, 1932). isolated a bacterial endophyte from the nodules as the causative organism of nodule formation. This discovery led to the practice of legume inoculation and the encouraged use of legume plants in crop rotation as an accepted practice essential for the nitrogen enrichment of Agricultural soils.

Many have asked the question, "why has not more been done with the nodulated non-legumes?" or, "are these plants really effective in nitrogen fixation?"

A review of the literature shows that the early investigations of many non-legumes, and particularly the trees and shrubs, were contemporary with the major studies of the legumes.

In 1829 Meyen (Fred et al, 1932) discovered nodules on the Alder of the Betulaceae. In 1876 Warming (Burrill and Hansen, 1917; Fred et al, 1932) observed nodules on species of the Elaeagnaceae and in 1886 Brunchorst (Burrill and Hansen, 1917; Fred et al, 1932; Allen and Allen, 1965) reported nodules on the roots of Bayberries of the Myricaceae. This is the group of plants with which Dr. Fessenden has done most of his work.

I would say that some of the major reasons that much of the research has been done on the Ceanothus sp. of Betulaceae, and Myrica sp. of the Myricaceae are because the nodules are large and readily found, and the plant is a heavy understory cover in many forested areas.

Major difficulties have been encountered in work with the non-legumes. These include the many unsuccessful attempts to isolate a causative organism and obtain reinfection or reinoculation.

The inability to gain successful reinoculation has perhaps been the greatest deterent in the work with many of the non-legumes.

Beal in 1890 reported nodulation of Rhamnaceae, and in 1897 Janse found nodules on the Casuarinaceae. Katoaka reported nodulation of Coriariaceae in 1930. By 1930 six plant families had been recognized as nodulated non-legumes. Interest seemed to fade in this group of plants for more than twenty years. (Fred et al, 1932; Allen & Allen, 1965; Bond 1963; Becking, 1970).

Considerable controversy seemed to exist in opinions regarding causative organisms of nodules in the non-legumes. The work of Hawker and Fraymouth (1951) was an attempt to resolve this controversy and led to a renewed interest in the non-legumes.

In 1953 Lawrence (Bond, 1963; Becking, 1970) reported nodules on species of the Rosaceae and in 1964 Allen (Allen and Allen, 1965) of Wisconsin found nodules on a species of the Ericaceae. This is the plant family to which manzanita belongs.

Up until eleven years ago, 1964, nodulation was recognized on some species of eight plant families of non-legumes. Two of these, Casuarinaceae and Coriariaceae are not indigenous to the United States.

Some of the historical background dates, including the names of early investigators, family, genus, and some species of nodulated non-legumes recognized to 1965 are shown in Table 1.

TABLE 1. Families and Genera (with some species[1]) of Angiospermae recognized as nodulated non-legumes as combined from several reviews and references.

Family Genus	Species[1]	Incidence[2]	Early Investigators of Genus and Species	References[3]
Betulaceae				
Alnus	glutinosa	25/35 (25)	1829 Meyen	Fred et al. (1932)
	glutinosa		1866 Woronin	Burrill & Hansen (1917); Fred et al. (1932); Allen & Allen (1965)
	glutinosa		1896 Hiltner	Fred et al. (1932); Burril & Hansen (1917); Bond (1963)
	glutinosa		1898 Hiltner	Fred et al. (1932); Bond (1963); Allen & Allen (1965)
Casuarinaceae[4]				
Casuarina	muricata	14/45 (35)	1897 Janse	Fred et al. (1932); Allen & Allen (1965)
			1915 Kamerling	Fred et.al. (1932)
	equisetifolia		1918 Miche	Fred et al. (1932); Bond (1963)
	triangularis		1933 Mowry	Allen & Allen (1965); Bond (1963); Becking (1970)
Coriariaceae[4]				
Coriaria	japonica	12/15 (10)	1930 Katoaka	Fred et al. (1932); Allen & Allen (1965); Bond (1963); Becking (1970)
	arborea		1958 Harrison & Morrison	Fred et al. (1932); Bond (1963); Allen & Allen (1965)
	myrtifolia		1958 Bond	Bond (1958); Bond (1963); Allen & Allen (1965); Becking (1970)
Elaeagnaceae				
Elaeagnus	--	9/45 (30)	1876 Warming	Burrill & Hansen (1917); Fred et al. (1932)
Hippophae	--		1876 Warming	Burrill & Hansen (1917); Fred et al. (1932)
Shepherdia	--		1876 Warming	Burrill & Hansen (1917); Fred et al. (1932)
Elaeagnus	pungens		1886 Brunchorst	Burrill & Hansen (1917); Fred et al. (1932); Allen & Allen (1965)
	angustifolia		1892 Nobbe, Hiltner et al	Burrill & Hansen (1917)
	angustifolia		1898 Hiltner	Burrill & Hansen (1917); Fred et al. (1932); Bond (1963)
	argentia		1910 Arzberger	Fred et al. (1932)

TABLE 1. (Con't.)

Family Genus	Species[1]	Incidence[2]	Early Investigators of Genus and Species	Reference[3]
Hippophae	rhamnoides	1/1 (2)	1934 Roberg	Bond (1963); Allen & Allen (1965); Becking (1970)
Shepherdia	argentea	2/3	1910 Warren	Allen & Allen (1965)
	canadensis	(3)	1957 Gardner & Bond	Bond (1958); Allen & Allen (1965); Becking (1970)
Ericaceae				
Arctostaphylos	uva-ursi	1/40 (0)	1964 Allen et al.	Allen & Allen (1965); Becking (1970)
Myricaceae				
Myrica (Comptonia)	--	12/35 (45)	1886 Brunchorst	Burrill & Hansen (1917); Fred et al. (1932)
	--		1890 Moeller	Burrill & Hansen (1917); Fred et al. (1932)
	sepida		1902 Chevalier	Allen & Allen (1965)
	rubra		1902 Shibata	Burrill & Hansen (1917); Bond (1963) Allen & Allen (1965)
	asplenifolia et al.		1910 Arzberger	Burrill & Hansen (1917); Allen & Allen (1965)
	gale		1911 Bottomley	Burrill & Hansen (1917); Fred et al. (1932)
	gale, cerifera et al.		1919 Youngen	Bond (1963); Allen & Allen (1965)
Rhamnaceae				
Ceanothus	americanus	30/55 (40)	1890 Beal	Burrill & Hansen (1917); Fred et al. (1932); Becking (1970)
			1910 Arzberger	Burrill & Hansen (1917); Fred et al. (1932); Allen & Allen (1965)
Discaria	toumatou	1/10	1958 Morrison & Harris	Bond (1963); Becking (1970)
			1961 Morrison	Allen & Allen (1965); Becking (1970)

TABLE 1. (Concluded)

Family Genus	Species[1]	Incidence[2]	Early Investigators of Genus and Species	References[3]
Rosaceae				
<u>Dryas</u>	<u>drummondii</u>	3/4 (0)	1953 Lawrence	Bond (1963) p. 72; Becking (1970)
	<u>drummondii</u>		1955 Crocker & Major	Allen & Allen (1965); Becking (1970)
<u>Purshia</u>	<u>tridentata</u>	2/2 (0)	1961 Wagle & Vlamis	Allen & Allen (1965); Becking (1970)
<u>Cerocarpus</u>	<u>betuloides</u>	1/20 (0)	1964 Vlamis <u>et al</u>	Allen & Allen (1965); Becking (1970)

[1] Only principal species upon which the very early investigation were made of each genus are listed here.

[2] <u>Incidence</u> refers to the ratio of species upon which nodules have been found to the number of known species as reported by Silver (1971). Numbers in parenthesis are numbers of nodulated species as indicated by Bond (1963).

[3] Reference here is made only to those early investigators of specific species in each genus. This is in order to avoid duplication of the same reference by many authors, i.e. Allen, Becking, Bond, Nutman, Silver, Stewart, and others. Less than 20% of the nodulated species are therefore referenced.

[4] Families not indigenous to most of North America.

In 1967, call it luck, accident, research, or whatever it may be, I discovered nodules on the roots of one of the western sagebrush plants, Artemisia ludoviciana on the hills near Morgan Utah (Farnsworth and Hammond, 1968). I hope that you can imagine the thrill and the excitement of this experience.

In 1968 Max Hammond and I found nodules on the roots of the prickly pear, Opuntia fragilis, of the Cactaceae on the sand dunes near Jericho, Utah.

Most of you have probably never seen the nodules on either sagebrush or cactus. Those on cactus roots are small, even smaller than the head of a pin, whereas those on Artemisia ludoviciana are more nearly the size and shape of those growing on soybeans.

Stutz (1969) found nodules on another species of cactus, Opuntia polyacantha. He isolated an organism which he characterized as a fungi.

In the nodulation of Artemisia ludoviciana we are dealing with a very interesting system. The nodules vary in size from that of a small pea to as large as a quarter. There is still a lot to be learned about this system. We have obtained definite acetylene reduction, as an indicator of nitrogenase activity. We have isolated a bacterial organism which has many characteristics of the Rhizobium. We have not been able to get reinfection and nodulation of plants grown in the greenhouse.

Clawson and I (Clawson, Farnsworth and Hammond, 1972; Clawson, 1973) observed nodulation of both Artemisia ludoviciana and Artemisia michauxiana. We also found nodules on the roots of Biscuit root , Bluebell, Indian paintbrush, Rabbitbrush, and Violet. Since my first observations of nodulation in the 1967, I have searched and looked for them each spring. It is a rather significant fact that we do not find them at the same time at any location from year to year. It appears that we are dealing with a very fragile system

and one that is particularly sensitive to conditions of temperature and soil moisture.

During the past two years most of our research has been carried on under a grant from the Desert Biome Program at Utah State University. When the Desert Biome Program was first established, the original modeling and hypothesis was primarily based on the concept that the desert system was "closed" so to speak and the desert system functioned largely to the extent that what nitrogen was there was being recycled.

Research situations are at times most frustrating. For the past two years we have had funding to assist but have really had difficulty in finding nodules.

We realize more and more that we are dealing with a very fragile system and I cannot overemphasize that the controlling interrelated factors seem to be soil moisture, soil and air temperatures and photosynthetic activity of the plants.

In these desert, range and forest ecosystems and particularly those of the desert we are apparently working with systems involving growth harmones, enzymes, and regulators many of which are still unknown. It would seem that the desert plants have such a built-in control mechanism that they are able to cope with and adjust to conditions of rapid, radical, and extreme environmental changes.

As one looks at the role of nitrogen fixation in shrubs along with their values for livestock feed one has to conclude that there is much we do not know about them.

For example: in the registration packet you received today there are two small brochures. One showing some of the functions planned for this new shrub laboratory and some of the possibilities in shrub improvement. The other a beautifully colored, well-prepared brochure showing, "Some Important Shrubs of the West." On Page 12 is a picture of snowbrush, Ceanothus velutinus known as one of the major nodulated non-legumes. On page 9, a picture of Rabbitbrush,

Chrysothamnus nauseosus. There are many others, but on pages 2 and 3 are pictures of bitterbrush, Purshia tridentata, also known to be nodulated and big sagebrush, Artemisia tridenta which is so useful in restoring big game ranges in Nevada and Utah. Under this picture is this statement which I call to your attention, "Many insects attack big sagebrush. Aroga moth has been responsible for complete elimination of this plant from some ranges. Other abundant and widespread insects produce galls on various parts of the shrub, which resemble fruits and flowers. These growths seem to cause no great harm, are not unsightly, and may eventually prove to have some worthwhile value."

These are also some of the research possibilities of the shrub lab. Today I am going to make comments and pose several questions which I hope may stimulate your research thoughts and start a few wheels of your mind to begin to turn to facets of the unknown answers and unsolved problems regarding shrub plants.

I have found nodules on the roots of sagebrush in this area from April 20 to as late as July 31. Two years ago in 1973 when we found nodulated roots on these plants on the Manti-LaSal Forest on July 6 I thought that this surely must be as late in the season as they will be found. This year, 1975, however, we found nodules from July 9 to as late as July 31. The nodules on July 31 appeared old, they were beginning to shrivel and were not effective in the reduction of acetylene; whereas the nodules on July 9 were active in the reduction of acetylene to ethylene.

Dr. Harold J. Evans, at Oregon State University has challenged us on some of our findings. He has indicated that he found nodules on sagebrush in Oregon but they are inactive in acetylene reduction.

Acetylene reduction has been widely accepted as an index of nitrogen fixation since the technique was developed by Hardy et al (1968) of the E.J. du Pont de Nemours and Co. We have found that the activity of nodules of Artemisia

ludoviciana and *A. michauxiana* in the reduction of acetylene is definitely affected by soil temperature and age of nodules.

During the remainder of my presentation I shall attempt to point out to you some of these inter-relationships and also to answer some of the challenges of Dr. Evans.

Figure 1 shows nodulation of *Artemisia ludoviciana* as first observed in 1967. These nodules are usually found one to three inches below the soil surface. In very stony areas we have found them near the surface. As I indicated earlier we have isolated a bacterial organism from these nodules which has characteristics of the *Rhizobium* spp., but we have not been successful in reinoculation or reinfection in the greenhouse.

Table 2 lists the names of plants in the families we have found to be nodulated. Also are listed species in plant families not previously recognized as being nodulated or only recently reported.

Dr. Evan Romney and Dr. Arthur Wallace of U.C.L.A. and I have collaborated on a paper which we hope will appear in the forth coming Synthesis Volume of the Desert Biome.

We also list there 20 plant families of the non-legumes which have been observed to be nodulated, see Table 2. Definite nitrogen fixation has not been established for all of these but the implications are strong that it does occur. Many have been shown to reduce acetylene and grow on soils of a very low nitrogen content.

If research is not followed through on these plants and extended to others we are overlooking the potential understanding of nitrogen fixation by many shrub plants on the desert, range, and forest soils.

Frischknecht (1963) reported in the Journal of Range Management some rather interesting findings regarding rabbitbrush. The work was done at Benmore where he found that forage production of crested wheatgrass when

Fig. 1 .--Close-ups of nodulated roots of Artemisia ludoviciana as first observed in 1967.

TABLE 2. Families and Genera of Nodulated Non-leguminous Angiospermae reported since 1965 as being nodulated, or previously reported[1] but not generally recognized.[2]

Family Genus	Species	Early Investigators of Genus and Species	References
Scrophulariacea			
Melampyrum	*pratense*	1888 Beijerinck	Mishustin & Shil'nikova (1968)
Rhinanthus	*major*	1888 Beijerinck	Mishustin & Shil'nikova (1968)
Castilleja	*chromosa*	1972 Farnsworth & Clawson	Clawson (1972; 1973)
Zygophyllaceae			
Tribulus	*terrestris*	1913 Isachenko	Lange (1966); Mishustin & Shil'-nikova (1968)
		1952 Montasir & Sidrack	Lange (1966); Mishustin & Shil'-nikova (1968)
		1972 Athar and Mahmoud	Athar and Mahmoud (1972)
Zygophyllum	*album*	1946 Sabet	Sabet (1946)
Zygophyllum	*coccineum*	1946 Sabet	Sabet (1946); Mostafa & Mahmoud (1951)
		1952 Montasir & Sidrack	Lange (1966); Mishustin & Shil'-nikova (1968)
Zygophyllum	*decumbens*	1946 Sabet	Sabet (1946)
Zygophyllum	*simplex*	1946 Sabet	Sabet (1946); Athar & Mahmoud (1972)
		1972 Athar & Mahmoud	
Fagonia	*arabica*	1946 Sabet	Sabet (1946); Lange (1966); Mostafa & Mahmoud (1951)
Tribulus	*alatus*	1946 Sabet	Sabet (1946); Lange (1966); Mostafa & Mahmoud (1951)
Tribulus	*cistoides*	1949 Allen & Allen	Allen & Allen (1950); Mishustin & Shil'nikova (1968)
Fagonia	*cretica*	1972 Athar & Mahmoud	Athar & Mahmoud (1972)
Rubiaceae			
Coffea	*rubusta*	1932 Steyaert	Lange (1966); Mishustin & Shil'-nikova (1968)
Coffea	*klainii*	1932 Steyaert	Lange (1966); Mishustin & Shil'-nikova (1968)
Gramineae			
Alopecurus	*pratensis*	1938 Nogtev	Mishustin & Shil'nikova (1968)
		1939 Mudrova	Mishustin & Shil'nikova (1968)

TABLE 2. (Con't.)

Family Genus	Species	Early Investigators Of Genus and Species	Reference
Poa	pratensis	1958 Savel'ev et al.	Mishustin & Shil'nikova (1968)
Clinelymus	sibiricus	1958 Savel'ev et al.	Mishustin & Shil'nikova (1968)
Clinelymus	ventricosus	1958 Savel'ev et al.	Mishustin & Shil'nikova (1968)
Cruciferae			
Brassica	--	1959 Schwartz	Mishustin & Shil'nikova (1968)
Raphanus	--	1959 Schwartz	Mishustin & Shil'nikova (1968)
Compositae			
Artemisia	ludoviciana	1967 Farnsworth	Farnsworth & Hammond (1968)
Artemisia	michauxiana	1972 Farnsworth & Clawson	Clawson & Farnsworth (1972); Clawson (1973)
Chrysothamnus	viscidiflorus	1972 Farnsworth & Clawson	Clawson & Farnsworth (1972); Clawson (1973)
Artemisia	tridentata	1972 Wallace & Romney	Wallace & Romney (1972)
Cactaceae			
Opuntia	fragilis	1968 Farnsworth & Hammond	Farnsworth & Hammond (1968)
Opuntia	polyacantha	1969 Stutz	Stutz (1969)
Boriaginaceae			
Mertensia	brevistyla	1972 Farnsworth & Clawson	Clawson & Farnsworth (1972); Clawson (1973)
Krameriaceae			
Krameria	parvifolia	1972 Wallace & Romney	Wallace & Romney (1972)
Umbelliferae			
Lomatium	triternatum	1972 Farnsworth & Clawson	Clawson & Farnsworth (1972); Clawson (1973)

TABLE 2. (Concluded)

Family Genus	Species	Early Investigators of Genus and Species	References
Violiaceae			
Violia	praemorsa	1972 Farnsworth & Clawson	Clawson & Farnsworth (1972); Clawson (1973)
Ulmaceae			
Trema	aspera	1973 Trinick	Trinick (1973)

[1] Listed in chronological order in relation to when a species of each family and genus was first reported.

[2] There are still differences of opinion as to whether or not the swellings (nodular growths) on the roots of some of these plants are nodules in the true sense of structure and effectiveness in symbiotic nitrogen fixation. Nodulation has been observed but the role in specific symbiotic nitrogen fixation of several of these has not yet been shown.

seeded directly in land covered with growth of rabbitbrush, Chrysothamnus nauseosus, was almost as high as when the rabbitbrush was removed shortly before seeding. Production of forage was also much greater than when the crested wheatgrass was seeded on land from which the rabbitbrush had been removed for several years before seeding. Some of these data are presented in Table 3.

My interpretation of these differences is based only upon circumstantial evidence. The implications are that rabbitbrush is most likely responsible for the nitrogen build-up in these soils. We have not observed nodules on C. nauseosus but we have found them on the roots of Chrysothamnus viscidiflorus. The major factor involved in the difference between treatments two and three could be a competition for moisture in the combined removal of moisture by rabbitbrush and crested wheat.

One other interesting bit of information which we have found is in the comparison of the total nitrogen content of alfalfa, sagebrush (Artemisia ludoviciana), rabbitbrush and greasewood. Normally alfalfa contains about 14.0 to 18.0 percent protein or 2.4 to 3.0 percent total nitrogen.

Our findings in Table 4 show that the nitrogen content of these three desert plants is considerably higher than alfalfa. The nitrogen content of greasewood has us somewhat baffled. It is so extremely high, 4.9 to 5.4 percent total nitrogen. We do not know whether greasewood is a nitrate accumulator or a nitrogen fixer. We have not observed nodules on the roots of this plant. This should be considered further in research projects. It could be a particularly valuable shrub if it were more palatable. However, sheep and some other animals will eat it if no other shrubs or browse are available.

TABLE 3

FORAGE PRODUCTION OF CRESTED WHEATGRASS WHEN GROWN ON LAND AREAS OCCUPIED WITH RABBITBRUSH (*Chrysothamnus nauseosus*)

Seeding sequence for Crested Wheatgrass	Yield of Forage K/Ha
1. Rabbitbrush removed several years prior to seeding	1,072
2. Rabbitbrush removed prior to seeding	1,818
3. Rabbitbrush not removed (Crested Wheatgrass seeded in rabbitbrush).	1,734

TABLE 4

NITROGEN CONTENT OF ALFALFA COMPARED WITH NON-LEGUMINOUS PLANTS

Plant Species	Percent Total Nitrogen[1]	Percent Protein (Protein Equivalent)
Alfalfa (*Medicago sativa*)	2.4 to 3.0	14.0 - 18.7
Herbaceous sagebrush (*Artemisia ludoviciana*)	3.3 to 3.8	20.6 - 23.7
Rabbitbrush (*Chrysothamnus vicidiflorus*)	4.1 to 4.6	24.6 - 28.7
Greasewood (*Sarcobatus vermiculatus*)	4.9 to 5.4	30.6 - 33.7

[1] Total nitrogen content was determined on 8 to 10 samples of each plant species collected in different areas of Utah, Nevada, and Wyoming in early June 1968 and 1969.

Back again to 1972. This was the year we were making some of our most encouraging progress. On May 4 of that year the nodules on Artemisia ludoviciana were highly active in the reduction of acetylene. The extent of this activity was of the magnitude of that of the nodules found on the roots of alfalfa, red clover, and sweet clover at that same time. This was in the range of 220 to 260 nanamols of ethylene produced per day per gram of fresh nodular material.

The acetylene reduction of Artemisia ludoviciana does not appear to be long lived under a desert environment. The activity declined rapidly the week after May 4 and had practically ceased by May 31. It would appear that there was about a month to perhaps five or six weeks of activity. The data showing this activity are given in Table 5.

This past spring we consistantly covered the area from the Desert Range Experiment Station, west of Milford, Utah, to Morgan, Utah and into Curlew Valley west of Snowville, Utah. We were unable to find any nodulation whatsoever. Over the past several years I have been able to find nodules either at Morgan or on the Manti-LaSal or at both locations.

On June 4, 1975 the new vegetative growth of Artemisia ludoviciana at Morgan had reached a height of 2 to 3 inches (about 5 to 7.5 cm). There had been no appreciable growth since April 30. This growth was quite insignificant when compared with the 12 to 15 inch (30 to 37.5 cm) height the growth was when I first observed nodulation there on May 28, 1967.

In 1974 a more careful study was begun of the conditions of soil moisture and soil temperature to see if a correlation could be established between nodulation and these factors. Figure 2 shows the relationships found to exist that year.

As we follow through the moisture - temperature changes in soil depths of 0-7.5 cm and 7.5-15 cm it can be seen that at the end of April or first of May the soil moisture content was rapidly decreasing and the soil temperatures

TABLE 5

PRODUCTION OF ETHYLENE FROM ACETYLENE BY VARIOUS ROOT NODULE SAMPLES

Sample type	Nanamols ethylene/mg fr wt nodule/day	*Mg fr wt nodule/sample
Alfalfa	229	1364
Red Clover	240	1461
Sweet Clover	247	1354
Artemisia ludoviciana 5/4/72	259	1450
Artemisia ludoviciana 5/11/72	38.8	1375
Artemisia ludoviciana 5/18/72	12.6	1463
Artemisia ludoviciana 5/23/72	.48	1372
Artemisia ludoviciana 5/30/72	.3	1495

* Milligram of fresh weight of nodule.

were increasing. From field observations in the past it had been observed that the most profuse nodulation seemed to occur when soil temperatures were between 5°C. and 10°C. This would also seem to indicate that the acetylene reduction is caused by a cool temperature activated enzyme system.

On Figure 2 I have blocked out the area between 5°C and 10°C as the Zone of Observed Nodulation. The upper limit of available moisture (field capacity) and the lower limit of available moisture (wilting percentage), for the soil at Morgan, are placed on the figure as straight line limits above and below the Zone of Observed Nodulation.

Evidently nodulation also requires sufficient plant growth early in the season to provide ample photosynthetic activity to supply the microorganisms with photosynthate necessary to carry on nitrogen fixation. It has been reported that approximately 60% of the photosynthetic product produced by the plant is used as energy in the process of nitrogen fixation.

Observe that as the soil temperature increased in the 0-7.5 cm depth the temperature line is outside of the area of the Zone of Observed Nodulation. Also, the temperature in the 7.5 to 15.0 cm depth is above 10°C soon after April 30. A similar pattern was found to exist in the field this spring, 1975. Consequently plant growth was practically at a stand still from May 1 to June 4. The Zone of Observed Nodulation of different soils, with respect to soil moisture content, would be positioned differently on the graph but the moisture - temperature relationships should remain the same.

It is conjectured that when the soil moisture and soil temperature are at such a level as to remain near together within the Zone of Nodulation, and there is sufficient vegetative plant growth to provide the required amount of photosynthate nodulation would occur on the root system. At the point whenever either the soil temperatures rise above 10°c. or the soil moisture content drops below the required moisture level the nodules dry and become inactive.

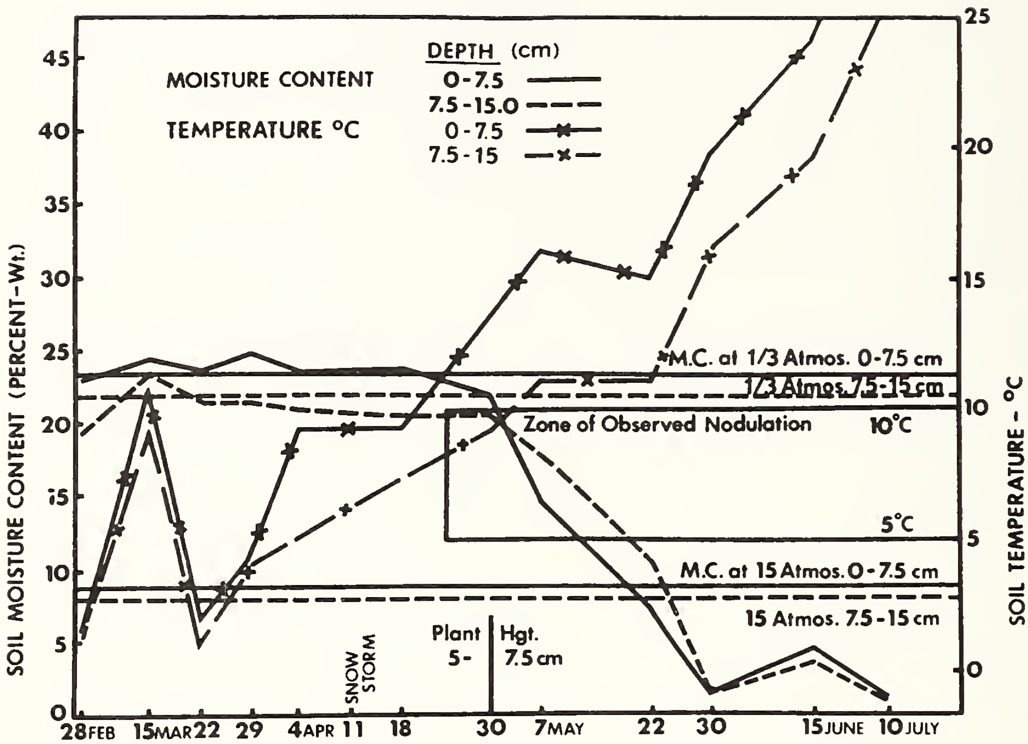

Fig. 2. Soil moisture-temperature-nodulation interrelationships, Morgan, Utah 28 Feb. - 10 July 1974.

As these environmental factors begin to change they apparently trigger some built-in control mechanism of growth regulators that allow for a plant to produce only sufficient vegetative growth and reproductive parts which will remain in balance with the amount of moisture and nutrients available to the plant.

As far as the nitrogen fixation system is concerned, the plant would therefore be able to fix only as much nitrogen as could be utilized by the vegetative portions in relation to the amount of available moisture. If the changes in the environmental factors are too rapid or extreme plants may either go dormant or die. These types of regulators, particularly in desert and range plants are probably quite different from those found in the crop plants. Through plant breeding and selection for high yielding crops man has perhaps eleminated certain of these natural growth control regulators.

On June 5 this year we found nodules on the roots of <u>Artemisia michauxiana</u> at Chester, Idaho. The plants were more than 30 centimeters (a foot) in height. The soil temperature was found to be 10°C and the soil moisture content was at 70% in the available range.

Figure 3 shows the comparative height of plants at Morgan, Utah June 4 with those at Chester, Idaho on June 5. Notice particularly the difference in plant size in relation to total area in relationship to photosynthetic activity. Soil temperature was warmer at Morgan so the difference in the plant growth is undoubtedly due to the difference in available soil moisture and the level of nitrogen evidently supplied by nodule activity.

On July 9, 1975, nodulation was found on <u>Artemisia michauxiana</u> on the Manti-LaSal Forest on the Philadelphia Flat area above Ephraim, Utah. The plants were 10 to 12 inches (25 to 30 cm) in height and exhibited some of the most profuse nodule development I have ever seen. Many of the nodules were almost as large as a quarter. The investigations at this location led to, what we believe to be, some very interesting and significant developments.

Fig. 3.Comparative height of sagebrush plants at Morgan, Utah June 4, 1975 (bottom), and at Chester, Idaho June 5, 1975 (top).

In 1972 when Mike Clawson and I were working on this project we would excise the nodules from the roots, place them in an incubation chamber which was a 50 ml. plastic syringe, fill the system with a gas mixture containing acetylene, oxygen and argon. These containers were then incubated in a cold chest from the time they were collected in the field until we returned to the laboratory for gas analysis. We were able to readily determine the reduction of acetylene to ethylene.

This year it was found that if the nodules were incubated at warm temperatures between the time of collection in the field and laboratory analysis there was no acetylene reduction.

A procedure was developed this spring where we brought the entire plant system (leaves, stems, roots, nodules) intact into the laboratory.

The plant roots were washed carefully in water, wrapped in cheese cloth and the entire plant placed in a 3-liter, wide-mouth Fernbach flask. Approximately 150 ml of a glucose-phosphate solution was placed in the bottom of the flask. The flask was stoppered with a No. 13 rubber stopper. Fifty mls of air were withdrawn from the flask and replaced with 50 mls of acetylene. The flask was placed in a water bath under special lighting. In this set up we were able to maintain the plant in an active condition for more than three weeks.

The initial temperature of the water bath was 22°C which was maintained for the first 20 hours. During this period no acetylene reduction could be detected. The temperature of the water bath was then dropped to 8°C and maintained between 8°C and 12°C. In 16 hours ethylene production was evident. Ethylene production increased rapidly in the next 48 hours and continued over a three week period when it ceased. Figure 4 shows the results of this study and the induction of acetylene-dependent production of ethylene by nodules of *Artemisia michauxiana*.

In the series of experiments the following plant systems were studied: (1) heavily nodulated plant roots, (2) roots with all but a few nodules removed, and (3) plants from which all of the nodules had been removed. We also found that the reaction was one of acetylene dependency. No ethylene or acetylene was produced in the system in which nodulated plants were placed in flasks completely devoid of acetylene. Statements have been made that plants under stress may produce both acetylene and ethylene. This was not found to be the case in our investigations. This entire system and set up is of course one we are continuing to study.

The results that we have obtained tend to show that we are involved with a cool-temperature activated enzyme system.

There are other aspects of this entire project that are most challenging. Two years ago Dr. G. Bond of Great Britian wrote to me asking for a speciman of the nodules with which we were working. He was preparing a paper for meetings at Edinburgh to report on the extent of nodulation of non-legumes throughout the world. Before he included Artemisia ludoviciana as a nodulated species he wanted to examine some of the nodules. It was late in the season but I searched the area and was able to find several on the Manti-LaSal area. These were sent to him in a bottle of formalin-acetic acid-alcohol preserving solution.

He later wrote to me stating that he had some reservations about reporting these as true nodulated non-legumes. The nodules were considerably different from any he had heretofore examined. They did not appear to have their origin from medulary tissue as in the case of the legumes, nor did they appear to originate in the cortex layer as has been observed on the nodules of the regular woody trees and shrubs. He suggested that this was an insect gall perhaps caused by a nematode.

Over the period of nine years I have examined cross-sections of young

nodules and had never been able to find nematodes. I have always been able to isolate bacterial organisms. Early in the spring there seems to be no unusual growths or organisms within the nodule.

So last year we continued to examine the nodular structure more completely and I found that as they became older, or later in the season, a small larvae could be found.

This year we determined to more carefully follow through the season on any internal changes in the morphological structure of the nodules.

As I have previously indicated we found nodules on July 9 on the Manti-LaSal forest after a long, cold, and snowy spring. These plants had profuse nodular growth and were found to reduce acetylene. As the plants in the field became older the time required for induction of acetylene reduction became longer. When the nodules became quite scenescent acetylene reduction could no longer be induced.

As the nodules became older we observed the development of larvae inside of them and a subsequent appearance of many larval cells. This is one of the most exciting results we currently have to report.

A quantity of the older nodules was brought into the laboratory where we kept them in a pint ice cream fiber container. In five days, as we removed the lid, out flew dozens of small winged insects. The lid was hurriedly replaced and remained for several days until the insects had expired. Upon further examination we found hundreds of these tiny winged creatures. Dr. Vasco M. Tanner and Dr. Stephen L. Wood of our Department of Entomology identified them as midges.

In Figure 5 is shown nodules as they were observed on July 9 when they were found to (A) be active in the reduction of acetylene; (B) show the development of larval cells, and (C) shows the small midges which emerged from the cells of the nodules collected July 31.

This development presents a most interesting phenomen with many unusual and unanswered questions: Is the formation and development of these nodules

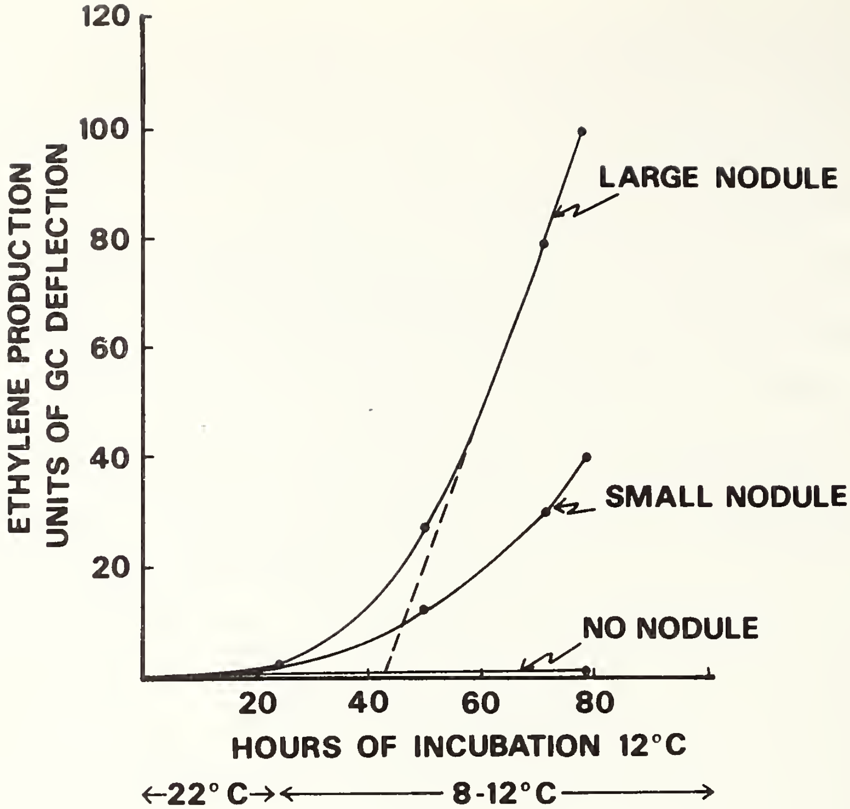

Fig. 4. Induction of acetylene-dependent production of ethylene by nodules on Artemisia michauxiana.

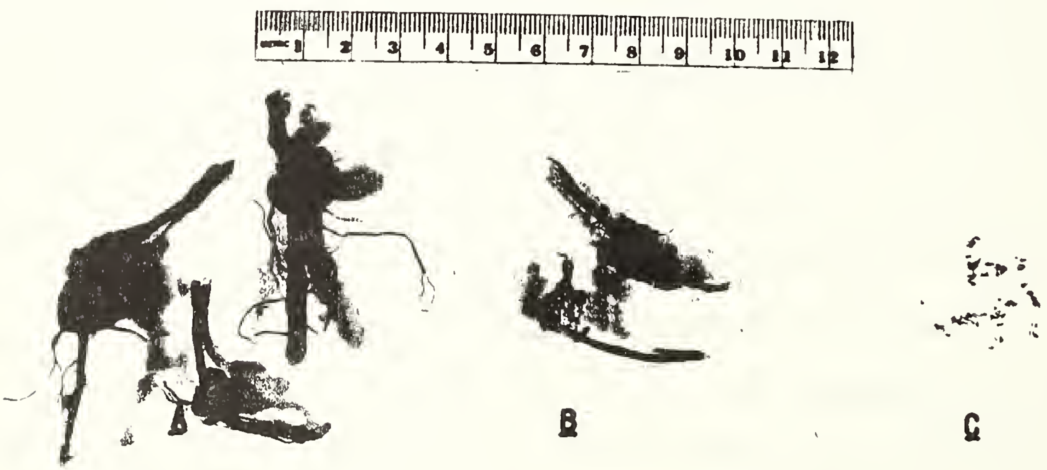

Fig. 5. Showing stages of root nodulation of Artemisia michauxiana (A) young active acetylene-reducing nodules, (B) larval cells of scenescent nodules from which midges (C) have emerged. Manti- LaSal Forest, July 9 -- 31, 1975.

a primary reaction from a bacterial infection, with the insect laying its eggs subsequentially into the nodule? Or, could this midge possibly be a "vector of infection?" Does it deposit its eggs simultaneously with the injection of the bacteria which produces the nodule which then becomes effective in nitrogen fixation, furnishing nitrogen to the plant and provides an environment and food for the larvae? Does the larvae and larval cells develop from a single egg with subsequent proliforation (probable paedogenesis), or from many eggs?

As of now we do not have the answer to any of these questions. One can only theorize. Since we have not been successful up to now in obtaining nodulation in the greenhouse, nor in the cool-zone-root growth chambers which we constructed over a year ago we are suggesting, and moving ahead in one phase of our research program that perhaps this insect is a vector of infection on some of these more woody shrubs.

Dr. Wood and Dr. Tanner have studied the midge and have classified it as belonging to the family, Cecidomyiidae. Dr. Wood sent specimen to some of midge experts in Washington, D.C. They concur in the family name. This is a family of insects known as "gall forming midges." They are recognized as causative agents of aerial galls on sagebrush, rabbitbrush, cactus and other desert and range plants.

However, they are not known to, nor are they supposed to go underground. The authority contacted was not completely sure that it could be catagorized in the presently recognized genus, which includes 20 species. It may be that this midge should be catagorized as a new genus as well as a completely new and heretofore unknown insect.

This brings me to again pose some unanswered questions: Is it possible that many of the range and desert plants, particularly sagebrush, rabbitbrush, and perhaps others have at least a three-way shunt path for nitrogen fixation? Could some of these insect galls be aerial nodules? Is it possible that there is an aerial process of nitrogen fixation, could nodulation of the roots be a

second avenue, and is the third nitrogen fixing activity of free-living or loose-symbiotic microorganisms in the rhizosphere? Many desert plants exhibit massive and intense encrustations which are difficult to remove or separate from the roots.

If the answer to the three-way question happens to be "yes" then there would be provided the mechanism of nitrogen fixation of different and varied environmental conditions.

I am intrigued with these possibilities and would surely encourage and plead for research along these lines. These are areas of possibility that have never been researched. The potentialities of this new Shrub Lab are tremendous.

It seems possible that as the insect oviposits its egg or eggs in the leaves, stems, or roots of plants that it could well inject a helpful bacterial organism carrying the "nif-gene" or the nitrogen fixing gene. The subsequent growth could be effective as a larval habitat and the nitrogen fixing unit for plants.

Perhaps it is time that we also began to seek for more specifically beneficial values and help from some of the insects.

In our observations of these aerial growths on sagebrush alone we have found a minimum of nine different kinds. Why? I simply do not know. Certain answers could be that this is because of the reaction of different subspecies of sagebrush to the same insect; or it might be that a different insect selects a different plant species. If this is so--what is the specific attractant responsible for this phenomenon? Is host specificity being exhibited here just the same as we find host specificity exhibited by the legume bacteria?

Figure 6 shows three of the many types of aerial growths which we have observed on other species of Artemisia. Some appear as small balls, others almost as cottony masses or flowers. Many of them exhibit an unusual oxidation-reduction enzyme system as can be observed by breaking open the nodule

Fig. 6. Some of the many forms and types of aerial growths (galls or nodules) found on species of *Artemisia*.

or gall and watch the color changes that occur as the interior is exposed to the atmosphere.

In conclusion let me say - there are so very many things which we do not know. I am hopeful that many of you scientists may supply the answers to some of the unanswered questions. Why are some shrubs more palatable than others as shown by the very splendid exhibit in the Shrub Lab? To what extent does nitrogen fixation really occur among this group of plants?

We have made some progress and shall continue to push forward in our small research way. I have often been asked just why I persist in research when I have so many other pressures in my University assignment.

I guess it is partly because of a desire to help unlock some of the secret doors of nature about us. It is an interesting area of research and I find it helpful and stimulating in my relationship with students. Too, I guess I found early in one of my experiences that one should not be easily discouraged in a research project until some one comes up with the answer and in some instances it may well be you.

When I was a student here at B.Y.U. many years ago--and then as I began my teaching career here at the University, Dr. William P. Martin and Joel Fletcher then at the University of Arizona believed that the algal crusts on the soil of the Arizona deserts were an important source of nitrogen fixation. Their department chairman did not agree and consequently would not allow them time for research on this project. William asked his father, Dr. Thomas L. Martin, here at B.Y.U. if we might be interested in this little research project. Dr. Martin of course said, "Yes," so William and Joel sent us a bag of algal crusts from Arizona.

Several of our students and I worked with Dr. Martin on this project for several months. We had what we thought were some exciting results.

The algae were grown in nitrogen-free media. After many isolations and transfers we were successful in isolating several strains of blue-green algae

that were fixing large quantities of nitrogen in the nitrogen-free media.

We prepared what we thought was a small but significantly informative paper. It was submitted to one of the major periodicals for publication.

Dr. O. N. Allen of the University of Wisconsin returned it to me and said that the reviewers had turned it down for the following reasons:

1. The paper was not scientifically well-written.
2. The findings were based solely upon laboratory findings and were not correlated with field work, and
3. Blue-green algae do not fix nitrogen.

Occasionally, I take out the manuscript and read those comments to remind me that concepts do change and perhaps one should not give up too quickly. Most generally it is persistance and perserverance in research that must be required before certain preconceived ideas can be changed and significant findings can be accepted.

It is now a completely accepted fact that blue-green algae are effective contributors in nitrogen fixation.

Now, may I say that I have presented some information but have posed many questions and related this story to point out to you that there are many areas in which we are yet just standing on the frontier of knowledge. Shrub research is one of these. You are the men who will reach out and explore these unknown regions. This new Shrub Laboratory may well be the means of helping in the search for new knowledge about shrubs, the future role they may play in nitrogen fixation and in helping to increase the food supply for a needy world.

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WOODY PLANTS FOR REHABILITATING RANGELANDS IN THE INTERMOUNTAIN REGION[1/]

Stephen B. Monsen and Donald R. Christensen[2/]

ABSTRACT

Studies dealing with the selection and propagation of woody plants for big game and livestock rangelands have demonstrated that a considerable number of native and exotic shrubs and trees can be successfully established within most major rangeland communities. The principal species used in rangeland plantings have been selected for their herbage and cover values, productivity, adaptability, and the success or ease of mechanical plantings and of rearing stock. Considerable variability among separate collections, ecotypes, and subspecies has been observed for most shrubs, and these differences have been used to promote the development of superior traits. The forage qualities of various shrubs have been markedly improved through the selection and propagation of palatable and productive collections.

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Plants that occur over a wide geographical range provide an extensive base of genetic material for breeding and selection. However, endemic collections have also demonstrated adaptability to a wide range of planting sites.

Most shrubs and trees have been successfully reared under nursery, greenhouse, and rangeland conditions. However, slow-developing shrub and tree seedlings are difficult to establish on arid sites. Steep slopes are also difficult to plant with conventional equipment. Most shrubs that are useful as forage plants have proved to be well adapted to restoring other wildland sites, particularly disturbed roadways, mine spoils, and recreation facilities.

INTRODUCTION

Shrubs and small trees are important components of the range resources in the western United States. Woody plants are distributed throughout nearly all vegetative communities, many times occurring as the principal constituent of major ecosystems, particularly in arid and semiarid regions. Often, shrubs are the only species encountered on halomorphic or salty soils. In addition, woody plants frequently reappear as pioneer species invading disturbed rangelands, roadways, and mine spoils. These aggressive invaders encourage the establishment of other desirable plants and provide important ground cover.

The shrublands of the western United States have been categorized into major types that occupy over 300 million hectares (Plummer 1975). Humphrey (1959) concluded that 50 percent of the total land area in Arizona supports woody plants, with shrubs being most prevalent in the arid regions of the State. Approximately 40 percent of all the forested habitat types described and classified by Steele and others (review manuscript, 1975) in central Idaho support shrubs as the principal understory plants in climax situations. Daubenmire and Daubenmire (1968) reported a slightly higher percentage of forest-shrub habitat types in eastern Washington and northern Idaho. Shrubs also occur in association with the major grassland communities of the Intermountain region. Bunchgrass frequently dominates foothill rangelands, yet shrubs occur in nearly all perennial grasslands (Christensen 1963).

Several shrub species are limited to specific environments within well-defined boundaries influenced by soils and climatic conditions. Others grow through a wide range of environments. A variety of ecotypes and biotypes have evolved within most species, partially accounting for the widespread distribution of many plants. Stutz (1972) described the Intermountain region as an important center for natural selection and evolutionary changes in the shrub complex. These processes have affected the distribution and modified important traits of many species. Consequently, a mosaic of vegetative types occurs throughout this region providing an array of plants that are adapted to a wide variety of sites.

Shrubs are important in the West not only because they occupy an expansive area, but because nearly all species provide food and cover for animal life and ground cover for soil stabilization. Big game depend heavily upon woody plants for forage and cover. Deer herds characteristically winter on shrublands, obtaining shelter and forage from woody species (Richens 1967). Elk depend to a lesser extent than deer upon shrubs for winter cover and forage (Boyd 1970). Bayless (1969) reported that antelope utilize woody plants in all seasons. Brandborg (1955) determined that mountain goats, wintering on the lower slopes of the Salmon River, subsist primarily on bluebunch wheatgrass (*Agropyron spicatum* and curlleaf mountain-mahogany (*Cercocarpus ledifolius ledifolius*).

Although conditions vary with individual herds, big game are often concentrated within the mountain brush, juniper-pinyon, or northern desert shrublands during the winter periods. Livestock also seasonally graze similar sites, spending the fall, winter, and spring periods on low foothills that usually are free of excessive snow. Large populations of grazing animals have weakened many shrublands, particularly in the last 100 years (Honess and Frost 1942; Julander 1958). Changes in the species composition of many shrublands have not resulted entirely from uncontrolled grazing. They have been brought about by other management practices including the suppression and use of fire (Biswell and Gilman 1961) and the impacts associated with converting rangelands to ranches, farms, and roadways. As early as 1924, Craddock and Forsling found that fluctuating climatic conditions greatly influenced the plant composition and herbage production of western shrublands. Their findings were reported in 1938.

Noticeable deterioration of western shrublands has been reported in the juniper-pinyon types (Reveal 1944), the northern desert shrub ranges (Pechanec and Stewart 1949), and the salt desert types (Hutchings 1966). These changes have seriously depleted the forage for big game and livestock. Consequently, emphasis has been directed to improving the forage conditions, particularly where juniper and pinyon trees have invaded these shrub communities.

Woody plants are also important to small animals including songbirds, raptors, and mammals. The management of sagebrush ranges to sustain populations of sage grouse has received considerable attention (Carr 1967). Deterioration of the grouse habitat recently led to research and management programs to maintain shrubs and trees essential to these animals.

At times, disease and insects cause severe damage to shrubs and trees. How much damage has been caused over the past 100 years by upset balances imposed by man is not known. Clearly, we must develop a better understanding of these factors as a basis for undertaking control measures where required.

SHRUB SELECTION CRITERIA

Selection of shrubs for range restoration has been based primarily on three criteria: (1) plants must be adapted to planting sites; (2) species must also provide such desired vegetative resources as forage, ground cover, and protection to animals; and (3) seedlings must be highly successful in establishing and surviving to maturity.

Considerable information has been acquired in each of the three categories. The ecology and distribution of most native shrubs have been well documented. Consequently, we can identify major sites where individual species are adapted and most likely to succeed (Beatle 1960; Nord 1965; Plummer and others 1968; Wood 1966). Also, the forage values and principal uses of many shrubs are known and provide guidelines for current plant selection programs (Kufeld and others 1973).

However, the limited use of most shrubs results from the lack of economically feasible methods of establishing them on large areas. Plummer and others (1968) described 21 factors used to rate the suitability of shrubs for planting. Nearly half of these characteristics relate to planting and plant survival. These are initial establishment, growth rate, persistence, germination, ease of planting, tolerance to grazing, compatibility with other plants, and ease of transplanting. Cultural practices that maximize seed germination and initial growth of young plants must be developed to increase seedling establishment.

To date, the principal shrubs that have proven successful in rangeland seedings are species that can be easily established and grow rapidly. Other shrubs that are difficult to establish are also being used with varying degrees of success. Certain highly desirable species are being propagated even though considerable attention is required to assure their survival.

The following criteria have been used in the initial screening of plants for revegetation of game and livestock ranges. Undoubtedly, other plant qualities must also be assessed and considered.

Species Adaptability

The principal criterion in the selection of shrubs for revegetation of rangelands is the ability of the plants to establish, to show acceptable growth, and to persist on the planting site. Consequently, native shrubs, which are naturally adapted, usually have been entered in the initial screening trials. Shrubs that occur in the mountain brush, juniper-pinyon, northern desert shrub, and salt desert shrub communities have received major attention to date.

Plants that are adapted throughout one or more of the major shrublands provide a genetic pool of plant materials useful in the revegetation of different rangeland sites. The subspecies of the big sagebrush complex, including *Artemisia tridentata* subsp. *vaseyana*, and *A. tridentata* subsp. *wyomingensis*, furnish a good base of planting stock. A number of subspecies, ecotypes, and biotypes of rubber rabbitbrush (*Chrysothamnus nauseosus*) also furnish a large reservoir of widely adapted materials. Ecotypes of winterfat (*Ceratoides lanata*), antelope bitterbrush (*Purshia tridentata*), fourwing saltbush (*Atriplex canescens*), and Woods rose (*Rosa woodsii*), have been selected for their ability to survive and grow satisfactorily within a fairly wide range of environments.

Shrubs that notably grow on specific sites are important to the particular kinds of areas on which they occur. For example, shadscale saltbush (*Atriplex confertifolia*), which often grows as a nearly pure stand on halomorphic or salty soils, is particularly adapted to these kinds of sites. Spiny hopsage (*Grayia spinosa*), longflower snowberry (*Symphoricarpos longiflorus*), and curlleaf mountain-mahogany also occur within narrow environmental gradients, but are vitally important forage plants for which substitutes having similar desirable attributes have not been found within their major areas of occurrence.

As expected, local collections have usually proven to be better adapted than introductions obtained from areas with different climatic conditions. However, significant success has been attained in planting some species beyond their native range. Selections of antelope bitterbrush from Janesville, California, have surpassed the growth rates of all other bitterbrush sources when tested on different sites in Utah and Idaho (fig. 1). In Utah, introductions of fourwing saltbush from cold climatic regions have survived extreme winter temperatures better than collections from the southwestern deserts (table 1). Recent studies by Van Epps (1975) strongly support these findings. The extension of Martin ceanothus (*Ceanothus martinii*) from its relatively restricted range in central Utah and eastern Nevada onto a variety of different soil types has been most encouraging. This shrub has exhibited adaptability to both acidic and basic soils and is growing equally well in the ponderosa pine and mountain brush habitat types in south-central Idaho. Successful plantings have also been achieved with green ephedra (*Ephedra viridis*), Apache plume (*Fallugia paradoxa*), Stansbury cliffrose (*Cowania mexicana stansburiana*), and wedgeleaf ceanothus (*Ceanothus cuneatus*) as introduced species on game ranges in Idaho. Introduced collections have also been bred with local collections to obtain improved progeny for future plantings.

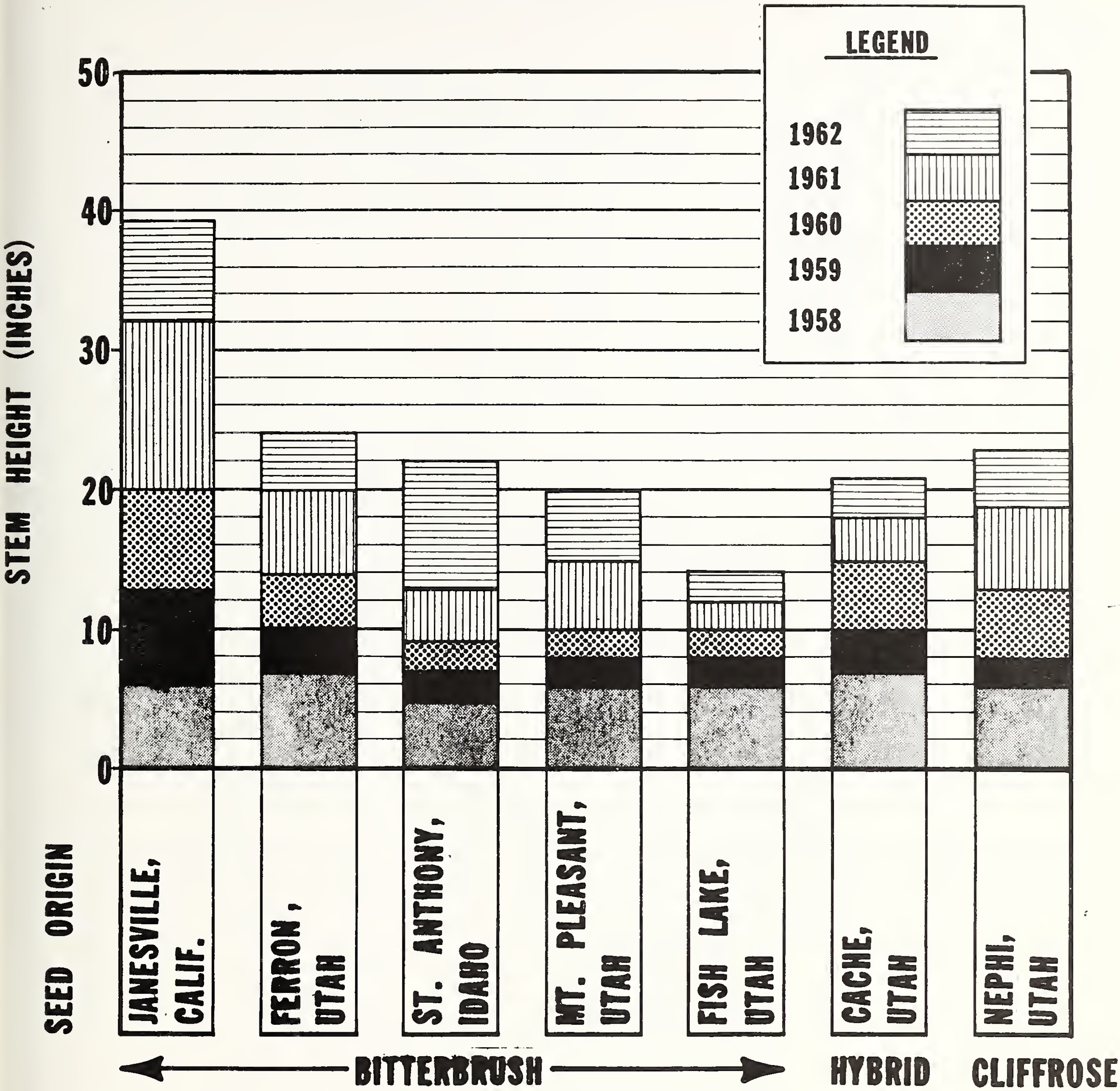

Figure 1.--Annual growth rates of selected sources of antelope bitterbrush, Stansbury cliffrose, and a bitterbrush X cliffrose hybrid grown at Ephraim, Utah.

Table 1. Annual herbage production for different sources of fourwing saltbush grown at Hobble Creek, Utah

Origin	Yield - grams per plant				
	1962	1963	1964	1965	1966
Wales, Utah	14	200	630	1,500	1,750
Tuba City, Ariz.	5	170	[1]120	450	950
St. George, Utah	15	150	[1]125	125	175
Carson NF, N.M.	16	290	570	1,550	1,500
Jackson Springs, Utah	4	125	[1]110	175	400
Buffalo Range, Ariz.	7	200	[1] --	--	--
Delta, Colo.	19	260	800	2,450	8,000

1/ Plants damaged by low winter temperatures.

Seed Availability and Ease of Handling

Unfortunately, the use of adapted shrubs is often stymied because seeds or seedling planting stock are not available. Seeds of most native shrubs are currently collected from wildland stands. Consequently, yearly seed crops are primarily dependent on annual weather conditions. Although the production of better quality seed of some species has been improved by rearing shrubs in cultivated nurseries, the inherent seed-bearing problems of other shrubs have not been overcome. For instance, fruit crops of fourwing saltbush and Wyeth eriogonum (*Eriogonum heracleoides*) collected from wildland stands normally yield approximately 50 to 60 percent or less viable or fully developed seeds (table 2). The production of a higher percentage of fully developed seeds has not always been attained even when plants are grown under cultivated conditions. Fortunately, fourwing saltbush produces an abundance of fruits or utricles, which compensates for the low percentage of filled seed.

Martin ceanothus produces few fruits or capsules, even under ideal conditions. The fruits are difficult to collect; however, in most years nearly all contain viable seeds. This shrub would be more widely used in large-scale range rehabilitation projects, if seed collection and production problems could be solved.

Table 2. Percent germination from dewinged utricles of different yearly collections of fourwing saltbush

Year of collection	Number of collections tested	Percent germination		
		Maximum	Mean	Minimum
1956	7	49	33	19
1957	19	52	39	14
1958	11	52	28	14
1959	11	67	41	19
1960	14	64	45	26
1961	11	69	40	17
1963	13	61	42	27
1964	7	37	35	28
1965	16	56	36	12
1966	5	52	35	17
1967	29	83	34	7
1968	10	60	47	37

The collection and handling of certain seeds, particularly curlleaf mountain-mahogany, can cause physical discomfort to the seed collector. Most shrub seeds can be cleaned and stored using conventional methods and machinery, although special equipment is required to handle seeds of irregular shape and to separate inert materials. However, equipment is not presently available to collect seeds of most shrubs, particularly if they are harvested from wildland sites.

Seed Germination

Shrubs are often planted on rangelands with herbaceous species. Usually, shrub seeds require a longer period of stratification than do the seeds of most herbs. Consequently, shrub seedlings are often suppressed by the more robust herbs. However, plantings of big sagebrush, rubber rabbitbrush, winterfat, antelope bitterbrush, green ephedra, Stansbury cliffrose, and fourwing saltbush have been successfully seeded with herbs as their stratification period is reasonably short or can be satisfied by artificial treatments. Other shrubs, including snowbrush ceanothus (*Ceanothus velutinus*) and true mountain-mahogany (*Cercocarpus montanus montanus*), require a long stratification period, but these plants can be successfully established if fall planted. Fall is generally suggested as the season for planting most shrubs.

Considerable progress has been achieved in the germination of many woody plants. However, the use of Rocky Mountain smooth sumace (*Rhus glabra cismontana*), roundleaf buffaloberry (*Shepherdia rotundifolia*), Woods rose, bitter cherry (*Prunus emarginata*), shadscale saltbush, and blueberry elder (*Sambucus cerulea*) has been restricted because of poor, highly erratic, or delayed germination responses (table 3).

Table 3. Percent germination of stratified shrub seeds maintained at a constant temperature of 6°C

Species	Duration of germination (days)							
	30	45	60	75	90	120	150	180
Buffaloberry, roundleaf	21	24	37	45	71	88	92	--
Chokecherry, black	--	--	53	63	65	81	--	--
Elder, blueberry	--	--	--	5	7	20	31	33
Peachbrush, desert	--	57	63	68	70	72	--	--
Serviceberry, Saskatoon	4	13	15	22	31	43	76	85
Serviceberry, Utah	1	19	40	51	72	90	95	--
Squawapple	2	19	24	26	30	32	49	96
Sumac, skunk bush	--	--	--	9	23	38	40	43

Seeds that germinate erratically often produce seedlings over an extended period. This trait may promote plant survival in some years or reduce the incidence of survival in others. However, if seeds are planted in a prepared seedbed, the optimum time interval for germination and emergence is important. In this instance, seeds are selectively placed in the soil, and plants should emerge on schedule to make optimum use of the available moisture. Scheduled emergence is important in nursery and greenhouse plantings since a precise period of germination insures the development of stock of uniform size and reduces maintenance and care of the seedbed or of germination chambers (fig. 2).

Ease of Establishment and Seedling Vigor

A most difficult task in establishing shrubs on rangelands is preparing a proper seedbed and eliminating competition from weeds. Weed reduction is often necessary for one or two complete seasons after planting. Slow developing shrubs are likely to succumb if weeds are not eliminated prior to seeding (Giunta and others 1975). Shrubs with aggressive seedlings are especially desirable, although seedlings (aggressive or not) of only a few woody plants are capable of establishing in closed stands of cheatgrass brome (*Bromus tectorum*) or perennial grasses. Shrubs with vigorous seedlings include antelope bitterbrush, sulfur eriogonum (*Eriogonum umbellatum*), snowbrush ceanothus, rubber rabbitbrush, big sagebrush, and fourwing saltbush.

Fourwing saltbush, rubber rabbitbrush, and big sagebrush have been successfully established when direct seeded with adapted grasses on arid rangelands in the Snake River Plain (table 4). These plants develop vigorous seedlings that are able to compete with seeded grasses. Consequently, these shrubs can be successfully established when simultaneously seeded in mixtures with herbaceous plants (fig. 3). Analysis of the growth responses of these shrubs seeded with perennial grasses has shown little or no correlation between shrub size or yields and the percent of understory herbs. Growth of the young shrub seedlings was not appreciably suppressed by the seeded grasses or by the annual weeds. However, planting shrubs directly into a well-established cover, including cheatgrass brome or cluster tarweed (*Madia glomerata*), is not recommended. Where shrubs are to be planted, other competitive plants must be controlled.

Seeding of shrubs with grasses and forbs has been successful. However, interplanting shrubs using the Hansen Seeder-scalper[3/] has aided shrub survival by placing seeds of the slower developing species in areas free of the seeded grass.

Often shrub seedlings have been severely weakened by the grazing of rodents, rabbits, and game animals. Plantings of antelope bitterbrush, Stansbury cliffrose, curlleaf mountain-mahogany, and blueberry elder achieved satisfactory stands amid a developing grass understory from broadcast seeding on bared mine spoils in eastern Idaho. The shrubs remained stunted and weakened from grazing for a number of years, but have recently increased in vigor and stature as game herds have been reduced.

[3/] Use of trade or firm names is for reader information only, and does not constitute endorsement by the U.S. Department of Agriculture of any commercial product or service.

Table 4. The number of shrubs established by direct seeding with herbaceous grasses - southern Idaho

Shrubs	Herbaceous cover	Number of shrubs per acre		
		Maximum	Average	Minimum
	Percent			
Rabbitbrush, rubber	60-70	14,000	8,240	5,100
Rabbitbrush, low	40-50	2,400	1,840	700
Sagebrush, big	40-50	1,800	440	160
Saltbush, fourwing	40-50	680	580	270

Figure 2.--In nursery plantings, seeds of most shrubs must be properly stratified to insure germination and the subsequent production of uniform transplanting stock.

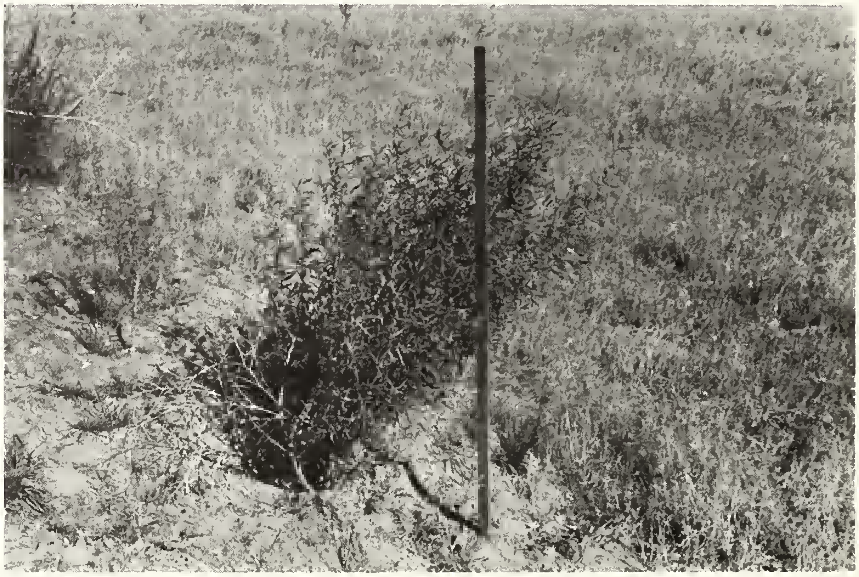

Figure 3.--Seedlings of fourwing saltbush grow rapidly and vigorously compete with understory herbs.

The growing periods of individual shrubs are important to their survival and persistence, particularly when competing for water with other plants. The period of maximum twig elongation and root development is often a key to the durability of young seedlings. Collections of desert peachbrush (*Prunus fasciculata*) and winterfat start to grow early in the spring and produce robust seedlings within a short time. Seedlings of green ephedra and sulfur eriogonum are able to survive in a dormant state if moisture becomes unavailable. Fourwing saltbush also grows rapidly as a young seedling, yet continues growth throughout the midsummer as other plants go dormant. In contrast, seedlings of Utah serviceberry (*Amelanchier utahensis utahensis*), blueberry elder, and Rocky Mountain maple (*Acer glabrum glabrum*) are most active in the fall if moisture is available. If planted in areas to which they are adapted, shrub and tree seedlings that survive the first or second summer normally become well established and do not succumb as young plants.

Growth Rates and Forage Production

Seeded shrubs that rapidly produce an abundance of herbage are particularly useful in the restoration of disturbed rangelands. Sites that are devoid of a woody cover but support less desirable vegetation must be converted to a more productive plant composition if game and livestock are to flourish. Consequently, shrubs that can produce an immediate cover in range rehabilitation projects can best prevent the reinvasion of weedy species and simultaneously produce a developing herbage base. Black locust (*Robinia pseudoacacia*), Tatarian honeysuckle (*Lonicera tatarica*), and Bessey cherry (*Prunus besseyi*) represent introductions that have been successfully used with native shrubs for this purpose.

The annual growth rates of some seeded shrubs grown on a pinyon-juniper site in central Utah are recorded in table 5. More rapid growth rates have been attained for some species at other testing sites.

Some plantings of Saskatoon serviceberry (*Amelanchier alnifolia*), black chokecherry (*Prunus virginiana melanocarpa*), and squawapple (*Peraphyllum ramosissimum*) have resulted in numerous seedlings that have failed to attain an appreciable size and have ultimately disappeared. However, these same plants are tenacious and persist on extremely harsh sites once they develop a reasonable stature. At maturity, they produce an excellent amount of forage even during years of low rainfall. Selection and breeding for rapid growth would greatly improve the potential for using these slower developing shrubs.

Table 5. Annual height measurements of seeded shrubs reared as cultivated plantings, Dahls study site, Ephraim Canyon, Utah

Species	Maximum height of the terminal shoot									
	1956	1957	1958	1959	1960	1961	1962	1963	1965	1968
	- - - - - - - - - - - - - - Inches - - - - - - - - - - - - - -									
Bitterbrush, antelope	5	8	13	26	29	32	36	25	48	--
Cherry, bitter	5	9	21	36	28	37	50	45	60	50
Chokecherry, black	2	4	12	44	48	51	62	65	80	84
Cliffrose, Stansbury	--	--	11	22	22	24	29	33	30	32
Currant, golden	5	13	25	58	60	61	65	72	96	90
Cypress, Arizona	--	--	12	12	17	22	25	27	30	52
Elder, blueberry	2	6	72	65	68	72	72	72	84	92
Mountain-mahogany, curlleaf	2	3	9	10	12	16	25	29	48	62
Mountain-mahogany, true	1	3	5	10	12	18	30	36	62	76
Peachbush, desert	3	6	19	20	23	27	36	40	34	46
Rabbitbrush, rubber	--	--	18	26	29	29	40	36	35	26
Rose, Woods	--	--	20	29	29	30	35	35	40	40
Sagebrush, big	2	10	16	26	36	40	47	50	52	54
Saltbush, fourwing	1	3	13	40	55	57	51	50	54	58
Serviceberry, Saskatoon	1	4	8	13	19	16	26	26	33	38
Serviceberry, Utah	1	3	19	26	26	26	26	26	30	30
Snowberry, mountain	5	15	16	26	27	29	34	36	50	45
Sumac, skunk bush	4	4	11	11	16	16	21	21	36	36
Winterfat, common	4	6	6	22	17	20	16	12	13	--

Quality of Herbage--Palatability Availability

Normally, the objective of rangeland plantings has been to provide forage for big game and livestock, and shrubs that are reasonably acceptable to these animals are being planted. Not all shrubs presently used for revegetation have been analyzed for their nutritive values, digestibility, or mineral contents. However, different ecotypes and subspecies of certain shrubs have been recognized that consistently are heavily browsed by game and livestock. Hanks and others (1973) detected chemical differences among different subspecies of big sagebrush, low sagebrush (*Artemisia arbuscula*), and rubber rabbitbrush through chromatographic analysis. Within the *A. tridentata* species, their findings reveal that big game and livestock decidedly prefer subspecies *vaseyana* and *wyomingensis* over subspecies *tridentata* (fig. 4). Of the rubber rabbitbrush collections tested, utilization is highest for subspecies *albicaulis* and *salicifolius*, less for subspecies *graveolens*, and least for subspecies *consimilis*.

Big sagebrush and rubber rabbitbrush have been criticized because of their apparent low palatability and general aggressiveness in establishing themselves in grasslands. However, through the detection of the more palatable subspecies of both genera, highly desirable sources can now be made available for rangeland improvement. Similar qualities can probably be detected and propagated in many other shrubs.

Through morphological comparisons, Stutz (1972) concluded that widespread hybridization has occurred between antelope bitterbrush and Stansbury cliffrose. Blauer and others (1975) successfully hybridized the two closely related shrubs. The distribution of Stansbury cliffrose was once more extensive than at present and resulted in natural crosses and populations with differing traits. Considerable differences occur in the palatability of antelope bitterbrush from collections obtained in the Intermountain region. The less palatable stands of antelope bitterbrush may be attributable to the genetic contributions from Stansbury cliffrose. Yet, the widespread distribution and differences in growth forms of antelope bitterbrush exist as usable sources for selection and development. Collections from the more mesic climates would likely be free of the Stansbury cliffrose genes as the more drought-tolerant cliffrose may not have extended into these regions.

Short and others (1966) concluded from analyses of important browse plants that seasonal changes in plant phenology and physiology are important to the nutrition and physiology of deer. The use of certain species is frequently dependent upon the abundance and quality of other plants. Plants that have been introduced onto western rangelands, unquestionably, have improved the composition and quality of the forage resource. This has been evident when Apache plume, wedgeleaf ceanothus, and Arizona cypress (*Cupressus arizonica*), moderately palatable shrubs, have been heavily browsed when planted in Idaho and Utah on areas outside of their natural range.

Availability

Shrubs are heavily browsed in the winter when herbaceous plants are dormant and often covered by snow. Woody plants that protrude above the snow, retain some leaves, or both are readily utilized. Erect shrubs such as curlleaf mountain-mahogany and snowbrush ceanothus provide excellent winter forage, although the low-growing creeping barberry (Berberis repens) and bush penstemon (Penstemon fruticosus) retain some of their leaves and are also selectively grazed if available (fig. 5).

Pruning or topping of curlleaf mountain-mahogany (Thompson 1970) and antelope bitterbrush (Ferguson and Basile 1966; Ferguson 1972) have been successful in providing more forage for grazing animals. Burning and chaining encourage the resprouting of certain shrubs and have also greatly increased the forage available to game. Hickey and Leege (1970) reported considerable improvement in elk habitat in northern Idaho through regeneration of redstem ceanothus (Ceanothus sanguineus) by controlled burning. The reestablishment of a desirable forage cover can also be attained by different planting methods; transplants of bittercherry, Woods rose, and scouler willow (Salix scouleriana) have grown rapidly, greatly exceeding their growth rates from direct seeding.

Figure 4.--*Artemisia tridentata* subsp. *vaseyana* (1) is selectively grazed by big game and livestock over *Artemisia tridentata* subsp. *tridentata* (2).

Figure 5.--Bush penstemon, a low-growing, semiwoody shrub, is often an important winter browse for big game.

Planting shrubs that retain succulence in midsummer is especially important to many arid rangelands in the Intermountain region. Seeding fourwing saltbush, green ephedra, and Gardner saltbush (*Atriplex gardneri*) in the northern desert and salt desert ranges provides this type of desired herbage.

Planting of *Eriogonum* and western virginsbower (*Clematis ligusticifolia*) in soils along ridges and around rocky outcrops produces important forage during critical periods when adjacent sites are covered with snow. These small, isolated areas, although used only temporarily, provide a variety of forage types and are vitally important to wintering animals.

RECENT DEVELOPMENTS IN PLANT SELECTION

Principal Species for Rangeland Plantings

Studies dealing with identification and selection of woody plants for rangeland sites in the Intermountain region have been reported by Holmgren (1959), Hubbard and Sanderson (1961), and Springfield (1970). Plummer and others (1968) characterized the qualities and uses of numerous species, particularly those useful in revegetating game winter ranges. The principal species selected through trial plantings that are being used more widely for restoration are listed in table 6. Morphological studies (Orsham 1972) and physiological investigations (Scott 1973) of individual shrubs are examples of associated studies that have aided the selection process.

Recently, chromatographic procedures developed and used to identify palatable subspecies of *Artemisia* and *Chrysothamnus* have been extremely valuable (Hanks and others 1973). Other less dramatic processes have been discovered and used to good advantage in the shrub-selection program.

Table 6. Successful shrubs for restoring principal western rangeland communities

Species	Areas of adaptation				
	Mtn. brush	Juniper-pinyon	Northern desert shrublands	Southern desert shrublands	Salt desert shrublands
Bitterbrush, antelope	x	x	x		
Bitterbrush, desert		x	x	x	
Ceanothus, Martin	x	x	x		
Ceanothus, snowbrush	x				
Chokecherry, black	x	x			
Cliffrose, Stansbury	x	x	x		
Elder, blueberry	x	x	x		
Ephedra, green		x	x	x	
Mountain-mahogany, true	x	x			
Rabbitbrush, rubber	x	x	x	x	x
Rabbitbrush, low		x	x	x	x
Sagebrush, big	x	x	x	x	
Sagebrush, black		x	x	x	
Saltbush, fourwing		x	x	x	x
Winterfat, common		x	x	x	x

Layering growth forms of antelope bitterbrush have been selected and used to improve the ground cover on unstable rangelands. Seedlings of the low-growing forms of antelope bitterbrush appear to be more competitive with herbs than do upright growth forms. Also, some selections acquired from forested communities grow rapidly when planted at lower elevations and appear to be well adapted to these drier sites. Collections obtained from neutral soil appear less sensitive to differences in soil pH than plant material acquired from strongly basic or acidic soils.

Recent collections of antelope bitterbrush from the sage-grass regions of the Snake River Plain have performed reasonably well when planted in arid regions. Although not adequately tested, this Idaho source appears to be fire tolerant which would further its use in fire disclimax areas. Collections of desert bitterbrush (*Purshia glandulosa*) are also highly fire tolerant and can be used in similar situations.

In the past few years, the selection of woody plants for use in the forest-shrub and salt desert shrub communities has been emphasized. Species are needed that will improve forage quality and watershed stability in both communities, and that will be useful in rehabilitating lands disturbed by grazing, recent mining activity, and road construction.

Collections of fourwing saltbush and common winterfat taken from the plains region in southern Montana and eastern Idaho appear better adapted to the mountain brush and big sagebrush sites than those from the desert regions of Utah and Nevada. Stutz (1975) reported a large form of fourwing saltbush from a localized site near Jericho, Utah. This is taller and much more robust than other ecotypes. If introduced to the arid rangelands where saltbush is adapted, herbage production could be greatly increased. Fourwing saltbush would certainly complement the sagebrush and mountain brush communities, particularly in south-central Idaho, if forms adapted to neutral and slightly acidic soils were available. Recent plantings indicate that some strains may be adapted to these soil types.

Rearing nursery stock of snowbrush ceanothus and Martin ceanothus has provided useful materials for planting the mountain-brush and juniper-pinyon sites. Although snowbrush ceanothus is usually encountered as a forest understory, the shrub is important to game herds. Often regarded as a weedy "brush" of little forage value, this species exhibits a variety of growth forms. Differences in palatability have also been observed. There are wide differences in ecotypes of this important shrub.

Although only two collections of Martin ceanothus, both obtained from the mountain-brush zone in central Utah, have been available for extensive testing, the stock has been widely successful. Plantings have been extended to acidic soils in Idaho and Nevada and to the sagebrush types in Utah and Idaho. The shrub grows rapidly, particularly in regions more arid than those in which it is normally encountered. This is certainly an important trait. It is an excellent browse plant and appears to be useful for restoration of low foothill and mountain-brush sites.

Seeding half shrubs or suffrutescent plants has improved the composition of forage plants on rangelands. To date, Wyeth sulfur and eriogonum and bush penstemon have excelled and provide quality browse. Both species of *Eriogonum* are common throughout the Intermountain States and are adapted to harsh, rocky soils. The plants are evergreen and are grazed year-round, thus improving the balance and quality of succulent forage. Prostrate kochia (*Kochia prostrata*), a semiwoody introduction from Russia, appears to be well adapted to the arid rangelands of the western States. The plant is very palatable and so is an important species for treating desert sites.

USE OF BARE-ROOT AND CONTAINERIZED PLANTING STOCK

The propagation and field planting of nursery- and container-grown shrubs have extended the use of many species (Ferguson and Monsen 1974). Most native shrubs can be reared as nursery stock and transplanted onto rangeland sites. This method of planting is more costly than direct seeding. However, Medin and Ferguson (1972) have been able to improve the forage for game by transplanting antelope bitterbrush and wedgeleaf ceanothus on steep unstable game ranges along the South Fork of the Payette River. Transplanting is particularly useful in reestablishing shrubs on sites dominated by cheatgrass and other weedy annuals.

Transplanting has also promoted the use of some shrubs that have been difficult to establish by direct seeding. Transplanting Stansbury cliffrose, Apache plume, desert peachbrush, and desert bitterbrush on arid rangelands has significantly improved the restoration of sites that are often difficult to treat. Utah serviceberry, blueberry elder, bittercherry, and true mountain-mahogany are often slow to develop from seeding, yet transplants of these species can be used to good advantage. If transplanting costs can be reduced through mechanization, this practice has great potential in range revegetation and particularly in the restoration of disturbed areas.

SHRUBS FOR WILDLAND DISTURBANCES

Although most early efforts in shrub research have been directed toward the development of forage plants for rangelands, recent disturbances by mining and road construction have required the use of similar plants for ground cover, erosion control, and esthetics (Monsen 1974). Many shrubs that have been propagated and developed as forage plants are excellent species for these disturbances. Less palatable subspecies of big sagebrush and rubber rabbitbrush have been selectively planted with fringed sagebrush (*Artemisia frigida*), black greasewood (*Sarcobatus vermiculatus vermiculatus*), and common wormwood (*Artemisia absinthium*) to discourage grazing on highly erosive soils.

Shrubs that are adapted to (1) infertile soils, particularly salt desert sites; (2) lithic outcrops; and (3) sandy soils have been especially useful in the restoration of exposed substrata from mining and road construction. Common winterfat and shadscale saltbush have been planted on strip-mined lands in western Montana, although the climate is somewhat more mesic than that in which these species are normally found (fig. 6).

Transplanting antelope bitterbrush, Russian olive (*Elaeagnus angustifolia*), skunk bush sumac (*Rhus trilobata trilobata*), common lilac (*Syringa vulgaris*), and Siberian peashrub (*Caragana arborescens*) on phosphate mine spoils in eastern Idaho has greatly improved the cover on sites once occupied by quaking aspen (*Populus tremuloides*) and bigtooth maple (*Acer grandidentatum*) (fig. 7).

Figure 6.--Common winterfat is a useful shrub for planting bare mine spoils in arid regions.

Interestingly, shrubs have been useful as cover crops for planting highly erosive road fills (fig. 8). Small shrub and tree transplants have significantly reduced erosion on road fills and stabilized soil conditions allowing grasses to become established (Megahan 1974). Transplantings of snowbrush ceanothus, oldman wormwood (*Artemisia abrotanum*), scouler willow, Woods rose, ponderosa pine (*Pinus ponderosa*), and mountain snowberry (*Symphoricarpos oreophilus oreophilus*) have done well on forested roadways (Monsen 1974).

Species that harbor nitrogen-fixing soil organisms have been useful, particularly for infertile soils. Collections of Louisiana sagebrush (*Artemisia ludoviciana*), a half shrub, are particularly promising in this regard (Farnsworth and Hammond 1968). Rooting habits of all subspecies are currently being investigated to select spreading types that provide better ground cover.

Snowbrush ceanothus and antelope bitterbrush have been reported as host plants for nitrogen-fixing organisms (Russell and Evans 1966; Webster and others 1967). Both shrubs are particularly adapted to infertile soils and have been successfully planted on abandoned dredge mines, roadways, and logging sites in central Idaho.

It is apparent that shrubs will continue to be valuable planting stock for wildland sites and will be used for purposes other than as forage and cover for big game and livestock.

Figure 7.--Transplants of antelope bitterbrush have proved to be well adapted to infertile mine spoils.

Figure 8.--Transplanted trees and shrubs on forest roadways have stabilized erosion and promoted the establishment of herbaceous plants.

FUTURE SHRUB RESEARCH

Research involving shrubs has been greatly expanded, particularly in the past decade. Information presently being developed in autecology, synecology, and physiology represents research that has assisted, and will continue to assist, the selection and development of woody plants for range revegetation. However, study areas that are related to the revegetation of rangelands and would provide maximum benefits are:

1. A more precise assessment of the adaptability and value of species and ecotypes presently on hand. Shrubs are not easily or quickly grown and evaluated. Consequently, years of field trials are required to document growth responses. Although numerous species and sources have been successfully used in rangeland plantings, the selection of suitable shrubs for this purpose is in an infant state. Further testing of all shrubs is needed to identify the site requirement and adaptation range of each species. The more promising shrubs, undoubtedly, should be considered first; yet, plants with a restricted range of distribution also deserve attention.

2. The selection and development of new strains and promising species should be actively pursued. This goal can be attained through selection and propagation of native and exotic stock and through a progressive breeding program. The development of specific traits in individual species could certainly advance their use in large-scale plantings. Especially needed is the development of planting stock with exceptional seedling vigor and rapid growth rates, particularly planting stock of such species as the mountain-mahoganies. Similarly, palatable sources of snowbrush ceanothus, bittercherry, and juniper would provide a significant base of usable forage plants. The genera of Fallugia, Ceratoides, Peraphyllum, and Atriplex are somewhat restricted to specific soil types and climatic conditions. However, these genera have distinct ecotypes that could be used to select more widely adapted planting stock.

A critical problem in the western States is the selection of plants that are adapted to arid conditions. Consequently, continued emphasis should be given to drought-tolerant sources of nearly all shrubs.

At present, selection and breeding appears to be most productive in promoting the forage qualities for the following taxa: Artemisia, Chrysothamnus, Atriplex, Amelanchier, Ceanothus, Purshia, Cowania, and Cercocarpus.

3. <u>The development of a dependable supply of high-quality seeds and transplanting stock</u>. Sufficient seed or planting stock is not currently available for any single shrub. Supplies are inadequate because seed orchards and nursery centers have not been developed and because difficulties in seed production and in the rearing of nursery stock have not been overcome. Regional farming and nursery operations must be developed to provide adapted stock for local use.

4. <u>Improvements in site preparation and planting procedures for the establishment of shrubs on rangelands</u>. The establishment of shrubs, particularly in association with herbaceous plants, has been a formidable problem on arid rangelands. Although erratic germination problems often contribute to seeding failures, competing weeds and improper seedbed preparation are the major factors preventing seedling establishment.

   Seeding and transplanting equipment is vitally needed to handle a wide assortment of planting stock. The Hansen Seeder has greatly aided in interplanting shrubs with herbaceous plants. However, at present, steep slopes, which often dominate rangeland sites, cannot be treated mechanically because existing equipment is inoperable on these sites.

Although methods of aerial seeding might be improved, equipment that will successfully control plant competition and actually place the seeds in a firm seedbed is needed. Also, machinery capable of operating on steep, rocky terrain certainly must be developed.

The cultural and handling practices that affect plant survival must be considered in the design and development of planting equipment. Such factors as optimum seeding rates, seeding depth, and methods of handling transplant stock warrant further research.

Nursery-grown transplants of desert peachbrush, bush penstemon, Wyeth eriogonum, and squawcarpet ceanothus (*Ceanothus prostratus*) are sensitive to improper handling. Plantings of container-grown stock of Arizona cypress and true mountain-mahogany greatly improve plant survival over plantings of bare-root stock. As these differences are detected, site preparation and planting methods can be significantly improved.

5. Reducing plant losses to insect and disease problems.
In selecting shrubs, resistance to insect depredation as well as to disease must be considered along with other plant characteristics. Little attention has been paid to the influence of insects and other organisms upon the growth, vegetative yields, and seed production of native shrubs. As shrubs are planted and reared in the nursery and in cultivated fields, insect and disease problems become more evident.

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SHRUBS AS CENTERS OF ADAPTIVE RADIATION AND EVOLUTION

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INTRODUCTION

In two previous publications (Stebbins 1965, 1972) I have proposed the hypothesis that the earliest, most primitive angiosperms were shrubs or sub-shrubs. The reasosn for favoring this hypothesis are as follows:

(1) The earliest angiosperms are more likely to have been woody than herbaceous, since all of the known non-angiospermous plants ("Gymnosperms" in the broadest sense of the term) are woody.

(2) Shrubs are favored over trees because many of them inhabit temporary, pioneer habitats, in which efficient reproduction by seeds, and in particular seed dispersal, has a particularly high adaptive value. A revolutionary advance in the efficiency of seed reproduction is one of the chief distinguishing characteristics of angiosperms.

(3) When certain groups of families are compared, particularly those in the orders Sapindales and Malvales, the families or tribes that consist entirely or chiefly of trees are more specialized in a number of characteristics than those that contain a high proportion of shrubs.

(4) Within certain families that consist chiefly of shrubs or herbs, (Ericaceae, Polygonaceae, Compositae) there exist a few genera that are trees. These genera are in every case more specialized than their shrubby relatives.

This hypothesis does not maintain that most modern shrubs, or even the majority of them, are more ancient and less specialized than modern genera and species of trees. The very fact that many shrubs inhabit regions in which high selective pressure exists for more efficient seed reproduction means that they probably have evolved more rapidly than trees, so that we would expect to find among various shrubby genera an entire spectrum of primitive, intermediate and advanced conditions. This is, in fact, what we find. Among the commonst shrubs in Australia and New Zealand are members of the primitive, vesselless angiosperm family Winteraceae (_Tasmannia_, _Pseudowintera_). The dominant shrubs of Pacific North America belong to families that are intermediate in their degree of specialization (Rhamnaceae, Ericaceae); while the Great Basin region is dominated by highly specialized shrubs belonging to the families Compositae and Chenopodiaceae (_Chrysothamnus_, _Arthemisia_, _Atriplex_, _Sarcobatus_). Occasionally, a single genus of shrubs contains relatively primitive species along with highly specialized ones. This is particularly true of the Australian genus _Hibbertia_ (Stebbins and Hoogland 1976a,b). The least specialized species belonging to this genus, with respect to their wood and their flowers, are among the least specialized of angiosperms. The most specialized ones are trailing shrubs that bear needle like leaves and flowers that are both reduced in numbers of parts and zygomorphic in symmetry.

Furthermore, the hypothesis that the earliest angiosperms were shrubs does not include or even imply the reverse hypothesis, that all shrubs are more primitive than related species that are trees or herbs. The term "shrub" is applied to all plants that are woody and do not have a central trunk,

regardless of other characteristics. This condition has been evolved many times and from many different ancestral growth forms. Some modern shrub species are descended from a continuous line of shrubby ancestors that goes back to the origin of the angiosperms; probable examples are the genera _Tasmannia_ and _Hibbertia_, already mentioned. Others, such as willows (_Salix_) and at least some species of oaks (_Quercus_), are probably derived from ancestors that were trees. Still others, such as the sagebrushes (_Artemisia_) as well as the saltbushes and their relatives in the Chenopodiaceae, are probably secondarily woody, being derived from herbaceous ancestors (Stebbins 1972). Consequently, one cannot discuss the evolution of shrubs as a group. Different genera of shrubs have had very different evolutionary ancestries.

ECOLOGICAL CONDITIONS MOST FAVORABLE FOR THE DEVELOPMENT OF SHRUB FORMATION

Ecologists are thoroughly familier with the fact that as ecological conditions deteriorate, shrubs tend to replace trees in more favorable climates and herbs such as bunch grasses under more severe conditions. The most meaningful classification of shrub habitats is, therefore, according to the stress factors that determine the severity of the environment.

The first of these is drought. Its effect can be seen most easily in regions like central California, where precipitation is marginal for forest development. In this region, many of the ridges that run east and west have forests or oak parkland on their north facing slopes and brush or chaparral on those that face south. In mountain ranges like the Santa Lucia Mountains south of Monterey, which are fissured by narrow canyons having precipitous sides, those facing northward support lush forests of redwood, while the south facing slopes opposite to them are covered with chaparral that consists chiefly of chamise (_Adenostoma_).

The second stress factor is inadequate mineral nutrients or water holding capacity of the soil. The effect of this factor can be seen most clearly in the transitional region of central California by looking at either a single hill slope that varies in steepness and depth of soil, or an area of lesser relief but caracterized by a sharp contrast in the bedrock or parent material underlying adjacent areas. In the hills east of San Francisco, as well as on the inner slopes of the Santa Lucia Mountains, the steeper slopes having shallow soil, that is often very poor in nutrients, support chaparral, while the gentler slopes support oak-parkland or foothill woodland. Many regions having gentler topography contain "ecological islands" of soil that is particularly poor in nutrients or even toxic to some plants, such as the sandstones of ancient sea benches or lenses of serpentine. Many of these "islands" are covered with shrubs while the surrounding regions, having better soils, support open woodland or parkland.

A third source of stress is fire. When forests are burned, particularly in regions having deficient moisture, they are replaced by shrub formations. In some regions, the shrub cover is so dense that without artificial reforestation the forest never returns, as in part of the Sierra Nevada of California. Elsewhere, there is a more or less regular successional return to forest cover. The fourth source of stress, grazing by domestic animals, is not discussed in this presentation, since its known effects have been in operation for such a short time that their influence on evolution of diversity in shrub communities cannot be estimated.

The three principal sources of stress interact with each other to such an extent that they cannot be considered separately. In regions of heavy precipitation as well as in deserts where drought stress is continuous, the effects of both topography and soil quality are much less marked than in transitional regions of intermediate precipitation. Fire exerts a maximum

effect in these transitional regions. In regions of heavy precipitation fires are more easily controlled, and recovery of the forest is less difficult, while the open formations of deserts, steppes, short grass plains or bunch grass areas do not have enough combustible material to support damaging fires.

Particularly in temperate or cold climates, three other sources of stress are important in promoting the development of shrubby vegetation: shade, poor aeration of sôil and winter cold. These stress factors produce shrubs having entirely different aspects from those of shrub formations resulting from drought, nutritional and fire stress. The leaves of arid or semi arid land shrubs tend to be thick and evergreen, while undershrubs in forests have thin, deciduous leaves. Their methods of seed dispersal are different, as is reviewed later in this presentation. Shrubs that inhabit the margins of swamps and other areas having waterlogged, poorly aerated soil may have had thick, evergreen leaves like those or semi arid areas (*Andromeda*, *Chamaedaphne*, *Kalmia*) or thin, deciduous ones (*Vaccinium*) like undershrubs of forests. The same is true of the prostrate shrubs of subarctic or subalpine regions.

FACTORS FAVORING THE DIVERSIFICATION OF SHRUB FLORAS

The extreme development of factors such as drought, poor soil, fire, shade and cold will increase the numbers of individuals of shrub species that have evolved tolerance of them, but by themselves do not promote speciation or evolution. A well known principle of evolutionary genetics (Stebbins 1950, Dobzhansky 1970) is that evolution proceeds most rapidly when populations are partially isolated from each other and are exposed to different or divergent environmental challenges. Consequently, the mosaic type habitats of regions that are transitional with respect to temperature and moisture,

that contain a mosaic of different soil types, and a much dissected topography are the most likely to be the laboratories of evolution and the cradles of new species and genera. Another factor is of primary importance in determining the number of species that exist in any region at any particular time: extinction vs. persistence of species. If, during a succession of geological epochs, a region has been subjected to continuous change by volcanic eruptions, glaciations, advance and retreat of seas, or elevation of mountain ranges, species may have become extinct as rapidly as they have been evolved so that in spite of rapid speciation, the flora at any time may not be very rich in species. On the other hand, if environmental change is followed by stability, extinction rates become low, and species diversity remains great.

These principles can be illustrated by comparing the shrub floras in different parts of the world. A shrub flora that is poor in species in spite of dominant associations and huge number of individuals is that of the sagebrush and salt bush plains that cover the northern Great Basin and the Columbia River drainage. As recorded in the list of Van Dersal (1938) and including his regions 7 (Palouse-Bitterroot Valley), 8 (Snake River Region-Utah Valley) and 9 (Great Basin-Intermontane), this flora contains only 178 species of shrubs belonging to 70 genera and 30 families (Table 1). The Pacific Coast Region (California, Oregon and Washington) is considerably richer. According to the flora of Abrams and Ferris (1923-1940), it includes 561 species of shrubs belonging to 135 genera and 41 families.

Although this latter flora contains four genera: *Ribes*, *Ceanothus*, *Arctostaphylos* and *Salix*, that appear to us to be rich in species, they pale into insignificance compared to the richness found in two regions of the

TABLE I. NUMBERS OF FAMILIES, GENERA AND SPECIES OF SHRUBS IN FIVE DIFFERENT FLORAS.

Region	Approx area (sq. miles)	Families	Genera	Species	Gen./Family	Spec./Genus
Intermontane Valleys, U.S.A (Van Dersal)	242,750	30	70	178	2.3	2.5
Pacific States, U.S.A. (Abrams and Ferris)	324,000	41	135	561	3.3	4.2
Chile (Reiche)	286,400	37	103	545	2.8	5.3
Western Australia, southwest half (Beard)	384,000	44	170	2624	3.9	15.4
South Africa (Thiselton-Dyer, Phillips)	472,800	64	336	3360	5.3	10.0

southern hemisphere, Western Australia and South Africa. Western Australia is one of the few parts of the world where natural wildflower displays are billed as a major attraction for tourists. A large proportion of the "wildflowers" are flowering shrubs. I have personally seen communities that contain forty to fifty different species of shrubs on a single acre; this condition is not unusual. These high numbers are not due to excessive splitting by Australian taxonomists. I have examined carefully one of the larger genera, Hibbertia, and find that its species are better differentiated than are those of Arctostaphylos and Ceanothus in California. I compiled the number of shrubs listed by Beard (1970) for the southwestern half of the state, which has an area smaller than that of the Union of South Africa and somewhat greater than the Pacific States. I included the South Western Province and the Eremean Province except for the Carnegie and Eucla Districts. This area contains 2624 species of shrubs belonging to 170 genera and 44 families. Four huge genera, Acacia (271 spp.), Grevillea (135 spp.), Melaleuca (105 spp.) and Leucopogon (99 spp.) contain together more species than the entire shrub flora of the Pacific United States.

An even richer region in South Africa. The Flora Capensis (Thiselton-Dyer et al 1894-1933), though old, is the best source of information; additional data were obtained from the survey of genera by Phillips (1951). South Africa contains about 3360 species of shrubs belonging to 336 genera and 64 families. Its area is somewhat greater than that of Western Australia and the Pacific United States. The two largest genera of this region, Erica (469 spp.) and Selago (112 spp.) contain together more species than the entire shrub flora of the Pacific states In spite of the opinions of

some plant geographers, the floras of these two continents have little relationship with each other. With respect to the two dominant families that they have in common, Johnson and Briggs (1975) have shown that the African genera of Proteaceae are not closely related to those of Australia, and the genera of Leguminosae are completely different in the two regions.

Since both of these shrub-rich areas are in the southern hemisphere, one might well ask: Is there anything about southern continents that promotes the evolutionary diversification of shrubs? A clear answer to this question, no,is provided by the flora of Chile. Although the flora by Reiche (1896-1911) is old and incomplete, it nevertheless provides enough information to be useful for comparison. It includes only 545 species of shrubs belonging to 103 genera and 37 families; numbers not very different from those obtained for Pacific North America. Although the area of Chile is smaller than those of the other regions tabulated, it could be made equally large or larger by adding temperate Argentina, for which no flora is available. Since this latter region is mainly grassland and contains few shrubs in addition to those on the slopes of the Andes, which for the most part occur also in Chile, a tabulation for all of temperate South America would probably include fewer than 600 species of shrubs. The pertinent question, therefore, is: "Why are the floras of temperate and subtropical America so much poorer in species of shrubs than the corresponding ones of South Africa and Australia?"

An answer to this question may lie in the different geological history of the four regions. During the latter part of the Tertiary Period as well as the Quaternary, The Cascade and Sierra Nevada mountains, as well as the

Andes, have been actively built-up, and in California and Oregon the coastal regions have seen the advance and retreat of continental seas. In addition, the effects of glaciation and periglacial phenomena have been profound. The temperate and subtropical regions of Pacific North and South America have therefore, been exposed to drastic environmental changes during the past 15 million years. By contrast, Western Australia has been extraordinarily stable (Crocker and Wood 1947). Neither mountain building nor glaciation have occurred, and due to the flatness of the terrain and the relatively slight differences between the soils of different regions, plants have been able to adjust to the relatively minor changes that have occurred largely by migrating into different areas (Marchant 1973). Although the rate of speciation does not appear to have been rapid, the rate of extinction has been even slower, so that many species have accumulated. South Africa has mountain ranges that are high in comparison to Australia, but much lower than the Andes or the highest Sierra Nevada. They are, furthermore, relatively old, and were not glaciated during the Pleistocene epoch (du Toit 1954). The diversity of terrain in South Africa is as great, but not greater than in Pacific North or South America; in all three of these regions the opportunities for speciation have been great. With respect to shrubs, the much richer flora of South Africa is due, I believe, chiefly to a lower rate of extinction.

If these speculations are supported by further observations, they will provide additional support for an hypothesis that I put forward recently (Stebbins 1974). The number and diversity of species found in a region is more likely to be a product of low vs. high rates of extinction than of high vs. low rates of speciation. Most regions that are rich in species

are both cradles of new species and museums in which old species are preserved. As a rule, however, the museum effect contributes more to the total number than does speciation by evolution.

ADAPTIVE DIFFERENCES WITH RESPECT TO PARTICULAR CHARACTERISTICS

I will now present a more detailed comparison between shrubs that occupy various kinds of habitats in central California, and show correlations between habitat and certain morphological or growth characteristics. The first of these is the ability to regenerate by stump- or crown-sprouting, in contrast to exclusive reproduction by seed. As Wells (1962, 1969) has pointed out, most shrubs can regenerate in this way. In California, the chief exceptions are in the genera *Arctostaphylos* and *Ceanothus*. The occurrence of both of these conditions has long been known (Jepson 1916). With respect to the pattern of distribution, in both genera the stump sprouters are most common in regions having a climate that is either equable with respect to temperature, mesic with respect to precipitation, or has both of these characteristics. The interior foothills, which are subjected to high summer temperatures and lower winter temperatures than the coastal areas, and in which in the absence of fog the summer drought is severe and prolonged, contain almost exclusively non-sprouting species in both (*A. viscida*, *A. manzanita*, *C. cuneatus*, *C. jepsonii*). As one ascends to middle altitudes in the Sierra Nevada, where contrasting temperatures prevail but the climate is relatively mesic, one encounters again stump sprouting species (*Arctostaphylos patula*, *A. nevadensis*, *Ceanothus velutinus*). The reasons for this difference are not clear. Wells (1969) has pointed out that the non-sprouters pass through many more generations during a given span of time than the sprouters. They also can be subjected to much stronger selection pressures,

since after each fire they produce huge numbers of seedlings, of which only a few can reach maturity. This is probably responsible for the fact that the majority of recently evolved, narrowly endemic species in both genera are non-sprouters. Since the Pliocene as well as the post-Pleistocene climate of California has been characterized by increasing aridity, newly available ecological niches have become more frequently available in the dry areas, and the genetic variability among the seedlings in the non-sprouters has equipped them best to evolve new combinations of genes adapting them to these new habitats. Possibly, this is the entire explanation for the greater success of the non-sprouters in the more arid inland areas. Nevertheless, the possibility also exists that non-sprouters are ipso facto better adapted to these conditions than are the stump sprouting species.

Particularly in the genus Arctostaphylos, a correlation exists between leaf size and adaptation to soil types. In several regions where two species occur sympatrically, a larger leaved species occurs on soils that are deeper, have a higher content of nutrient minerals, or both; while a smaller leaved species occurs on an adjacent poorer soil. Examples are presented in Table 2. The reasons for this correlation are more obscure than that for the one related to stump sprouting, mentioned above. Since small leaves are associated with more slender twigs, perhaps both of these adult characteristics are products of a smaller amount of meristematic tissue, which could be a more economic pattern of growth in association with a lower availability of mineral nutrients. To a certain degree, this difference extends to the total species composition of California brushlands. The ubiquitous shrub, Adenostoma fasciculatum or chamise, characteristically thrives in more sandy or shallower soils than associated species of Arctostaphylos or Ceanothus, which have much larger

Table 2. Pairs of sympatric species of Arctostaphylos that differ in leaf size and habitat preference.

Location	Larger leaves, On less Sterile soil	Smaller leaves, on more sterile soil
Mendocino County	*A. columbiana* Piper	*A. nummularia* Gray
Mt. Tamalpais, Marin County	*A. virgata* Eastw.	*A. montana* Eastw.
Mt. Tamalpais	*A. crustacea* Eastw.	*A. nummularia* var. *sensitiva* (Jeps.) McMinn
Santa Cruz Mountains	*A. Andersonii* Gray	*A. silvicola* Jeps. and Wies.
Monterey Peninsula	*A. tomentosa* (Pursh.) Lindl.	*A. hookeri* G. Don.
El Dorado County	*A. viscida* Parry	*A. nissenana* Merriam
Napa County	*A. manzanita* Parry	*A. stanfordiana* Parry
Ione, Amador County	*A. viscida* Parry	*A. myrtifolia* Parry

leaves. Another factor, temperature of the leaf surface, may contribute to this correlation. Gates et al (1968) have shown that in hot climates, small leaves retain temperatures similar to that of the surrounding air, due to free circulation, while large leaves, may absorb enough solar radiation to lift their temperatures several degrees above ambient temperature. Heat damage under these conditions can be avoided only by elaborating protective cuticles, which would be an additional drain on the synthetic capacities of shrubs inhabiting sterile soils.

Another characteristic that is correlated with climate in the evergreen vs. the deciduous condition of the leaves. I have elsewhere (Stebbins 1972, 1974) pointed out that in climates like that of central California, having marginal amounts of frost, deciduous trees and shrubs occupy more mesic sites, and drier sites are occupied by broad leaved evergreens. This condition is explained by the fact that leaf fall "hardens" plants and prepares them for periods of frost. In the drier sites the "hardening" of shrubs is an inevitable result of the dryness of their habitats. This correlation does not exist in either of the southern continents that I have visited, temperate South America and Australia, for the simple reason that deciduous trees and shrubs are virtually absent from their floras. Apparently, climatic and edaphic conditions in the southern hemisphere have rarely been favorable for the evolution of the deciduous condition, so that even at timberline in the mountains of central Chile, southeastern Australia, Tasmania and New Zealand the woody flora consists entirely of broad leaved evergreens, with the addition of a few evergreen conifers.

The conspicuous difference between the climates of the two hemispheres

is that because of the higher ratio of oceans to land mass the climates of the southern hemisphere are for the most part more insular, having lesser extremes of seasonal temperature than those of the interior parts of Eurasia and North America. Consequently, my hypothesis about the origin of the deciduous habit can be amended and shortened to state that the principal environmental stimuli to its evolution were the seasonal fluctuations in temperature that prevailed in the interior of the northern continents, beginning during the middle of the Tertiary period. The woody plants affected were primarily those inhabiting mesic sites, since in such situations the evolution of the deciduous condition had the double advantage of hardening them during the autumn, and increasing their dormancy as a protection from the winter cold.

CORRELATIONS BETWEEN METHODS OF SEED DISPERSAL AND HABITAT

I have elsewhere (Stebbins 1974) emphasized the importance of seed development, dispersal and seedling establishment for the evolutionary differentiation of angiosperm species, genera and higher categories. I know of no comparative studies of either seed development or seedling establishment on related species of shrubs. Methods of seed dispersal can, however, be recognized on the basis of morphological characteristics. I have, therefore, classified the shrub species of central California with respect to these methods, and the data are summarized in Table 3. By far the commonest method is the production of fleshy fruits or berries that are dispersed through ingestion by birds or other animals, and excreted at varying distances from the parental shrub. This is in striking contrast to dispersal methods in both the arboreal and the herbaceous species of

Table 3. Relationship between habitat and methods of seed dispersal in shrubs of Central California.

Habitat	Wind		Ingestion		No obvious method: large		No obvious method: small		Total
	no.	per cent	no.	per cent	no.	per cent	no.	per cent	
Dry scrub	2	1.8	41	37.9	49	44.5	18	16.4	111 spp.[1]
Wet scrub	5	41.7	6	50.0	1	8.3	0	0	12 spp.
Dry forest	0	0	29	76.4	6	15.8	2	5.2	38 spp.[2]
Wet forest	5	20.8	15	62.8	1	4.1	2	8.2	24 spp.[3]
Total	12	6.5	91	49.2	57	30.8	22	11.9	185

1 One species, the myrmecochrous, Dendromecon rigidum, is not included. See text.

2 One species, Holodiscus discolor, has plumose styles that may be adapted to either wind or adhesion.

3 One species, Cephalanthus occidentalis, has buoyant fruits that may be transported by flotation.

the same region. Of the 38 species of trees found in the region only 4 or 10 per cent have fleshy fruits. The remainder are equally divided between those having wind dispersed fruits or seeds and those having large fruits or seeds without obvious methods of dispersal, but which are often transported actively by birds or small mammals (acorns of *Quercus*, nuts of *Juglans* and *Aesculus*, van der Piji 1969). No data have been gathered on dispersal mechanisms of central Californian herbs, but in them both fleshy fruits and wind dispersed propagules are rare. The majority bear either small seeds having no obvious method of dispersal, or propagules that are either spiny, bristly or sticky and adhere to animals or the clothing of humans.

A little reflection can show how its particular predominant method of seed dispersal is adapted to the optimal evolutionary strategy of each of these life forms. In temperate regions, where winds are frequent, the taller trees bear flowers or cones on branches that are high enough above the ground so that the propagules can be caught up by the wind and blown for considerable distances; this is not true for the undershrubs. Also, in the deep shade of the forest floor, large seeds having large quantities of stored food are at a great advantage, since the seedlings do not have to rely exclusively upon photosynthesis until they are well established. Such seeds are too large to be eaten by the majority of birds that inhabit these forests; hence the adaptiveness of fleshiness and color as attractants for birds is greatly diminished.

Shrubs, on the other hand, cannot place their seeds in positions that are advantageous for wind transport. For most of them large seed size does not have a great selective advantage, since new establishment is usually under successional conditions, when light is available. Moreover, they

provide nesting sites and cover for many species of birds, so that the shrubs having bright colored berries are most likely to have their seeds dispersed by means of ingestion and excretion.

Among the numerous species of herbs that inhabit central California almost every mechanism of seed dispersal is represented. Some of those that inhabit forests (Clintonia, Trillium, Fragaria) have fleshy fruits like their shrubby associates. Others have wind dispersed propagules, while a large proportion produce small seeds that lack obvious dispersal mechanisms. Nevertheless, one of the commonest kinds of seed dispersal mechanisms in herbaceous species of this region includes spines, bristles, hooks, sticky seeds, or other devices that cause the propagule to adhere to fur, feathers or clothing. Such mechanisms are rare or lacking in shrubby species. Apparently, the most important vectors for propagules of herbaceous plants are small mammals or grazers that carry the seeds in their mouths or about their heads. Such vectors are much more available to low growing herbs than to taller shrubs.

Table 3 shows also that shrubs growing in different habitats include different proportions of the various adaptations. The species of dry scrubland, chiefly chaparral, include a majority of those having no obvious means of transport. One kind of adaptive complex that is rare among shrubs of the northern hemisphere is that favoring transport of seeds by ants, or myrmecochory. This method was believed to be confined to forest loving herbs until Berg (1966) found it in the bush poppy, Dendromecon. More recently (Berg 1975), he has found it to be widespread among the shrubby species of Australia. Possibly, other chaparral species having small

seeds take advantage of seed eating ants or other insect vectors, even though they do not possess any specialized attractive devices for this purpose.

The shrubs inhabiting the moister sites, chiefly streambanks, in areas of chaparral or other kinds of scrub include such a small number of species in central California that not much can be said about them. The group is dominated by willows, which have entered these habitats secondarily, and have retained the characteristic of small, wind dispersed seeds.

The undershrubs of drier forests include an overwhelming majority of species that have either fleshy fruits or large seeds adapted to dispersal by small animals, or without obvious dispersal mechanisms. This is quite in keeping with the abundance of vectors in such habitats. In the wetter parts of the forests the abundance of willows increases the percentage of wind dispersed seeds, as in brushlands.

CONCLUSION

Since the shrub category is not a natural one, but a collection of unrelated plants having similar growth forms, the biological and evolutionary problems associated with shrubs are not substantially different from those associated with plants in general. Nevertheless, many groups of shrubs present problems of particular interest, which deserve more

attention from botanists.

SUMMARY

Since shrubs are a growth form rather than a natural category, they have evolved in several different ways. The original angiosperms were probably shrubs, but some modern groups of shrubs have evolved from arboreal ancestors, and others from herbaceous ancestors. Still others are direct descendants of primitive shrubs. Plant associations dominated by shrubs develop most often in semi arid regions having poor soil; but many shrubs of temperate regions are undershrubs in forests. Stress conditions imposed by drought, inadequate mineral nutrition, fire and in some regions poor soil aeration and prolonged cold favor high proportions of shrubs in plant associations. Comparison of the richness of shrub floras of the Pacific United States, Chile, Western Australia and South Africa indicates that the most influential single factor in promoting diversity of a shrub flora is long time geological stability, bringing about a low rate of species extinction. Diversity of habitat is the second dominant factor. In at least one genus, Arctostaphylos, reduced leaf size is correlated with adaptation to poor soils. The deciduous condition has evolved in regions having a climate characterized by great fluctuations in temperature, and mild to heavy winter frosts, and in shrubs or trees adapted to wetter sites. In contrast to the condition in either trees or herbaceous plants of temperate regions, the commonest adaptation to seed dispersal in shrubs is the development of fleshy fruits or berries, that are eaten and excreted by birds or other vectors.

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Section II -- Contributed Papers

Modes of Adaptation to Desert Conditions in Chrysothamnus

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Rabbitbrush species (Chrysothamnus) are apparently well-suited to the desert or semi-desert environments of western America. Interestingly, the structural basis of adaptation to drought differs among the species. All species have relatively narrow leaves with low surface area-volume ratios that reduce heating by solar radiation. Stems and leaves of *C. nauseosus* are covered with a close felt-like layer of trichomes which insulate the plant and reduce transpiration. Leaves of *C. greenei* and *C. pulchellus* are glabrous but have very heavy cuticles. Several species, such as *C. viscidiflorus* and *C. albidus*, produce a sticky exudation that coats the leaves and young stems--this increases light reflectance from the plant surface which protects the plant from overheating. The protective felt-like cover on stems of *C. nauseosus* is maintained for two or three years before cork is produced. In those species lacking this tomentum, cork production is precocious and deep-seated in origin. Wood production is normal in most species; however, xeromorphy is probably related to development of interxylary cork in *C. greenei* and *C. viscidiflorus*. Polyploidy is found only in the latter species (with diploids, tetraploids, and hexaploids present). The polyploids occur either at lower latitudes or altitudes and appear better adapted to drought than are the diploids of *C. viscidiflorus*.

Studies of Insects that Infest Redstem Ceanothus in Northern Idaho with Particular Reference to Seed Production

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Redstem ceanothus, Ceanothus sanguineus Pursh., is a valuable component of brushfields on big game winter ranges. In northern Idaho, redstem comprises 60% of elk diet. It also ranks high in nutritive content.

Redstem ecology has been under study by the Idaho Fish and Game Department since 1964. More recently, we combined our interests and have surveyed dozens of insects and one gall mite that infest redstem. Many of these insects were not previously recorded from redstem, and our list is still incomplete.

Because insects were often immature in their damaging stage, they have been difficult to specifically identify. Descriptions of immature insects are rarely available; keys to their identities are critically needed.

The high cost of obtaining sound seed and the lack of information on insects that affect seed production have caused us to begin focusing attention on this particular aspect of redstem entomology. So far we have collected two caterpillars that destroy inflorescences (Filatima sperryi Clarke; Gelechia mandella Busk.). Seed are destroyed on the plant by larvae of an unknown weevil and by a phytophagous wasp, Eurytoma squamosa Bugbee. The latter has been collected by A. P. Plummer and K. R. Jorgensen from Ceanothus martini and Ceanothus greggii A. Gray. These are the first records of this insect from Utah and from those hosts. Plummer reported that the wasp prohibited collection of sufficient seed for planting.

We are presently developing methods of sampling and diagnosis for evaluating seed loss. Radiography of mature seed to supplement dissection is under investigation to determine its utility.

C_4 Photosynthesis and CAM Metabolism in Shrubs

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C_4 dicarboxylic acid pathway of photosynthesis has now been reported to be present in plants from a wide range of genera and at least 15 families in both the monocots and dicots. Current theory suggests that C_4 photosynthesis was originally an adaptation to bright, hot, and arid environments. Occurrence of C_4-plants in mesic or cool climates is thought to be due to migration. In addition since most C_4-plants now known are herbaceous, it has been suggested that C_4-shrubs and trees (Pearcy and Troughton, 1975) are relatively recent in occurrence. However, in many instances, these same herbaceous plants are considered on morphological grounds to be recently evolved; thus presenting a paradox.

Crassulacean acid metabolism (CAM) occurs in many succulent plants and represents another snydrome of adaptations to life in the desert. CAM plants are concerned with water conservation rather than efficient photosynthesis. Again CAM plants appear to be herbs or shrubs from at least 18 families.

A survey of C_4 and CAM-plants using data from this and other laboratories will be presented. Growth forms will be noted as well as possible evolutionary origins and trends. The ecologic role and evolutionary significance of CAM and C_4-shrubs will then be discussed.

Propagation of Callus Cultures and Attempts of Regenerating Intact Plants from Callus of Native Shrubs

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Plant improvement by asexual means has been proposed in recent publications and research in this area is being done in several laboratories. Improvement of native shrubs might also be accomplished by this means. As part of a long range program of plant improvement by asexual means we are attempting to regenerate plants from plant callus cultures preparatory to protoplast fusions and plant cell transformations via uptake of exogenous DNA.

We have in callus culture, five species of Atriplex, one species of Eurotia, one species of Artemisia and one species of Sarcobatus. Methods of obtaining and maintaining those callus cultures will be discussed. Three species of Atriplex have been selected for attempting regeneration from dedifferentiated callus tissue into intact plants. Conditions for the regeneration of roots will be reported. We are presently working on conditions for regeneration of shoots and roots simultaneously and our progress will be reported.

Some Growth Relationships of Creosote Bush (Larrea tridentata) in the California Desert

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Creosote bushes in the deserts of the Southwest develop doughnut shaped clones on several types of substrate. This growth pattern is clearly evident from aerial photos. Clones may reach sizes up to 25 m in diameter and represent genomes of extreme age. The slow growth of the clones is evident from: 1) matched aerial photos covering a span of 27 years; 2) constant differences in population structure (i.e. clone size) above and below the shoreline of lake Cahuilla whose last stand was approximately 400 years ago; 3) carbon-14 dates (up to 700 yrs BP) of remnant wood left behind as the rings expand outward, and 4) observation of growth habit in terms of annual increment and direction of size increase. Extrapolated ages of the larger clones yield estimates of several thousands of years. Isozyme analysis show that most large circular clumps with hollow middles are indeed clonal in origin and not the result of multiple seedling establishments.

Soil properties are markedly affected by the persistence of the slowly expanding plant canopy. Associated water repellant layers in the soil result in "water harvesting" on a microscale so as to markedly alter the soil-plant moisture regime.

The growth relationships determined for Larrea appear to be rather closely duplicated in many other species of arid land shrubs.

The Influence of Selected Native Rodents on Selected Plant Species in a Mormon Tea-Grass Community

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The effect that three species of native rodents have on selected plant species in a Mormon Tea-Grass community was studied in two ways. First, food preference of the Kangaroo rat (*Dipodomys ordii*) for several plant species within an enclosure was examined. Second, *D. ordii*, *Onychomys leucogaster* and *Ammospermophilus leucurus* was each placed in a separate enclosure surrounding the experimental plant, either *Gutierrezia sarothrae* *Eurotia lanata* or *Ephedra viridis* and the interactions were measured daily. In experiment one, based on the order of seed collection in the semi-desert community, the Kangaroo rat preferred the seeds of *Oryzopsis hymenoides* but readily took *Gilia* seeds and flowers when *Oryzopsis* seed was absent. The leaves of some *Festuca octoflora* were also eaten by the Kangaroo rat. In the second experiment, there was variation in the influence that rodents had upon most plant species studied, but insofar as we could determine, none of the animals tested ate *Gutierrezia sarothrae*. The Kangaroo rat and grasshopper mouse had a significant influence on *Eurotia lanata* preferring the young vegetative stalks and fruiting stocks that were in flower. The Antelope ground squireel (*Ammospermphilus leucurus*) in its attempt to escape, broke off most of the *Ephedra* and *Eurotia* stems so no accurate data could be gathered.

Rabbits Show Different Preferences According to Saltbush (Atriplex) Species and Strains

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There are over 400 shrub and herbaceous saltbush species or taxa in the world, many of importance because they provide palatable and nutritious browse, fodder or habitat conditions for livestock, big game and upland game birds. They are also useful to reduce fire hazards, stabilize disturbed soils, and for landscaping. Methods have been developed to establish several saltbush species on wildland sites by direct seedings. More extensive use has been drastically impaired by rabbits and certain rodents clipping and destroying these plants especially when young. Repellents have shown little noticeable effect except for short periods to reduce clipping. More widespread use would result if saltbush species or strains could be found that resist animal depredation.

A study designed to determine susceptibility of selected saltbush species and strains to clipping and subsequent damage especially by rabbits was carried out on a fuel-break cleared of chaparral brush at the North Mountain Experimental Area in Riverside County, California. Six native and two exotic species with 1 to 5 strains of each, and in some instances both juvenile and 1-year-old potted transplants were exposed starting at different dates to animal use during the first growing season. They were examined systematically to ascertain the degree of use and effects caused by rabbits clipping the plants.

Results showed that small animals, especially rabbits, had a distinct preference for certain species and strains. These preferences applied to

both small juvenile seedlings or larger plants throughout the first growing season. Species or strains originating from more distant locations or dissimilar sites were generally clipped earlier and to a greater extent than those from nearby sources or sites similar to the test area. Clipping intensity on Australian and Mediterranean saltbushes (*A. semibaccata* and *A. halimus*), exotic species that are naturalized in some parts of this country, averaged more than 75 percent as compared to less than 50 percent on most strains of allscale and four-wing saltbushes (*A. polycarpa* and *A. canescens*), both natives. In most instances, use was significantly lower on both allscale and fourwing saltbush strains that originated in California than from strains of these two species emanating from other states. Plants were either destroyed or severely stunted by clipping use above 75 percent. Although rabbit clipping is an important factor in establishing and growing saltbushes, selecting species or strains that are least preferred by these animals is a partial solution to the problem. It is important in propagating saltbush to use the species and strains adapted to the site and if possible, seed should be from a nearby source or from sites similar to the area being planted.

Variability in Natural Populations of Atriplex canescens

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The range of Atriplex canescens extends throughout the western United States, northern Mexico, and into southern Canada. The species is characterized by both intra- and interpopulational morphological variation. Its importance as a native forage plant and suggested potential as an agronomic crop has led us to investigate its ecotypic variation. It occurs in soils varying from non-saline to extremely saline, and we have selected ecotypes representing this habitat range for salt-water stress investigations. Mature plants from non-saline, moderately saline, and highly saline soils have been transplanted to the greenhouse. Rooted cuttings were cloned from these parent plants and established in liquid culture representing a full-strength Hoagland's solution, and Hoagland's supplemented with 0.25 M or 0.50 M NaCl.

The results suggest that survival in nature under saline conditions has led to selection for individuals tolerant of salt, and those plants have a selective advantage under artificial saline conditions. Such ecotypes might well be selected for planting as a forage species under a specific saline soil or saline irrigation water regime.

Germination Studies of Atriplex

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Low germination of Atriplex seeds appears to be due to (1) low seed set, (2) insect and microorganism predation of filled seeds, (3) genetic factors, and (4) mechanical and chemical inhibitors. Low seed fill in randomly collected seed lots is probably the result of (1) reduced pollination which is commonly inherent in such dioecious species, (2) biased samples which ordinarily will include an inordinate proportion of infertile or immature seeds because field collections will almost never be at the moment when the majority of seeds are at their optimum stage of development, and (3) genetic factors which interfere with normal development. The much lower germination of filled seeds in tetraploid Atriplex canescens than in diploid A. canescens suggests that genetic factors are also responsible for development beyond seed fill. In addition to the independent mechanical barriers furnished by fruit bracts and seed coats, a strong water soluble, chemical inhibitor is carried in the bracts and testae of most Atriplex species.

Because most populations of shrubby Atriplex contain a few monoecious plants, and because striking genetic differences in germinability are conspicuous among different Atriplex species, selection can almost certainly greatly increase the proportion of filled and germinable seeds. Simple separation techniques such as floating off empty seeds in ethanol and grinding of the fruits to remove the constricting bracts, give promise of abundant opportunity to improve germinability of Atriplex seeds to a point where their use in range reseeding programs will be economically sound.

The Usefulness of Shadscale in the Revegetation of Disturbed Sites in the Salt Desert Shrub Type

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In recent years native shrubs have received much consideration in range restoration, fire plantings, conservation, and mining revegetation programs. To date little success has been obtained from numerous plantings made in the salt desert shrub ecosystem. Although several species common in this type have been grown successfully in higher elevation deer winter range areas, comparatively little information is known about which species or ecotypes are best adapted to the salt desert shrub type and how they might be artificially propagated.

One such plant, uniquely adapted to this region, is *Atriplex confertifolia* or shadscale. Perhaps no other species of saltbush has a greater assortment of ecotypes and shows the amplitude of ecological tolerances as does shadscale. Of particular interest is the recent discovery of one strain of shadscale that may attain a diameter of 2.5 meters and persist in unstable environments by means of vegetative stem layering.

Shadscale is a dominant plant covering 13,000,000 hectares of the west. Shadscale demonstrates wider tolerances to soil textures, salinity, and temperatures than any other species of *Atriplex*. Due to the broad expanses where it is dominant, it is ecologically the most important *Atriplex* species found in North America.

Shadscale is especially tolerant of drought, being able to withstand moisture stresses that often kill less xeric species. Studies have demonstrated that shadscale is still photosynthetically active at moisture stress levels of -115 bars. In addition to this adaptation to

physical drought shadscale is well adapted to withstand physiological drought. The species has been reported to tolerate salt concentrations several times higher than the salt levels of the oceans.

The fertility levels of shadscale soils are usually low in total soil nitrogen. This adaptation to low fertility indicates that extensive programs of fertilization frequently recommended in many revegetation guidelines may be unnecessary on disturbed sites resulting from mining and highway construction.

Among the Atriplex species, few demonstrate the ecotypic variation shadscale has which adapts it to a range of soil textures. Although this species prefers heavy soils, it is also common on soils containing up to 70% sand. This broad range indicates shadscale has an extremely wide tolerance to soil oxygen levels in addition to soil moisture levels.

Although attempts to propagate this species have been reported as early as 1878, little is actually known about the artificial propagation of this species. Propagation from direct seeding has usually resulted in poor seedling stands, but more often than not outright failure. The planting of wildlings usually gives the best chance for survival, but results have not always been successful. Recent attempts at propagating this species from stem cuttings have been most promising. Rooting success is usually near 100% when cuttings are taken in the fall or early spring and rooted in a medium with good aeration such as commercial peat pellets.

Establishment of shrubs in the salt desert type will likely be realized in the future only through the use of bare rooted transplants or containerized outplantings. Such techniques lend themselves readily to present greenhouse plant production methods and will likely become more common in the future if success is ever realized in revegetation efforts in the salt desert shrub zone.

Drought Tolerant, Low Growing, Low Maintenance Shrubs for California Highways

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This is a summary of a 5-year Plant Materials Study between the California Department of Transportation, Sacramento, and the USDA Soil Conservation Service, Lockeford, California in cooperation with the Federal Highway Administration, Washington, D.C. Until the acceptance of the final report the author is responsible for the facts and accuracy of the data. Emphasis was placed upon drought tolerant, low grazing, low maintenance shrubs for revegetation, bank plantings and screens. Priority areas for work were in the foothills near San Francisco and along the Sierra Nevada Mountains, Lake Tahoe Basin and vicinity in the Sierra Nevada Mountains and Alturas in northeastern California. Emphasis was placed on native shrubs using container grown stock although other methods of establishment such as planting bareroot stock, direct seeding and the spreading of topsoil containing dormant shrub seeds were explored.

Many shrubs were propagated and established. The time has been too short to establish longevity rates or maintenance requirements. The better species at lower elevations were coyote brush, fourwing saltbush, California buckwheat, whiteleaf manzanita, buckbrush ceanothus, and rock rose (an exotic). Two narrow endemic and one naturally occurring hybrid ceanothus are being studied. At higher elevations, promising natives were sulfur flower buckwheat, mountain pride penstemon, squaw carpet ceanothus, big sagebrush, rubber rabbitbrush, mountain whitethorn, antelope bitterbrush, greenleaf manzanita, and red dosier dogwood; non-natives were Bandera rocky mountain penstemon, Caucasian sagebrush,

bearmat manzanita, prostrate summer cypress, two varieties of Arctic willow and common lilac.

Bareroot stock established nearly as well as container grown stock in limited trials. Excellent to poor results were obtained by spreading topsoil containing dormant seed over disturbed areas. Direct seeding was the least successful method. Pilot fertilizer and irrigation trails were conducted. Some species such as creeping sage and saltbushes responded more to slow release nitrogen and phosphate fertilizer than buckbrush ceanothus and whiteleaf manzanita. Little or no response was found to irrigating the first year using the schedules and amounts of water. The greatest problem in shrub establishment at lower elevations was competition from annual herbaceous species. Mice and grasshopper depredation must be controlled.

The Amount of Blackbrush in the Natural Plant Community is Largely Controlled by Edaphic Conditions

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A four year study of a large relict area (approximately 20,000 acres) located along the south rim of the Grand Canyon in Arizona has provided considerable information on the ecological amplitude of blackbush, Coleogyne ramosissima.

These plant communities, developing without the influence of man and his domestic livestock and where wildfires and other natural influences have been allowed to function, are widely variable. Blackbrush ranges from nearly pure stands to conditions where it makes up less than 10 percent of the total annual yield. Some sites exist where blackbrush becomes non-existent even though it is completely surrounded by plant communities containing blackbrush. In these situations fourwing saltbush, Atriplex canescens, becomes the dominant shrub.

Vegetative data has been collected from each study site for three separate years to identify the variability in yield by species and the percent composition within the plant community.

Detail soil information has been collected at each site to determine the physical properties such as depth to bedrock, type and condition of the bedrock, thickness and differentiation in soil horizons by structure and texture. Soil tests to indicate alkalinity, salinity, calcium carbonate and bulk density were made at each horizon of the soil profile.

A total of nine distinctly different edaphic conditions were identified. Evaluation of the vegetative data indicated there are five separate and distinct plant communities containing blackbrush in the study area.

Four diverse soil profiles produced plant communities predominantly blackbrush. Soil profiles with similar characteristics produced consistently similar plant communities. The study area was large enough to permit the study of the same soil type several times and thus determine the variability of the plant community for the same soil taxonomic unit. Conditions of the bedrock for the lithic soils had a pronounced effect on the amount of blackbrush in the plant community. Natural fires in areas where blackbrush predominated did not materially alter the plant community, i.e. these areas reverted immediately back to blackbrush without going through an intermediate plant association.

The study of this large relict area has provided needed data to determine range condition on nine major soil taxonomic units in the blackbrush climatic zone. Also, as a result of this study, it is now known that many of the areas now occupied by nearly pure stands of blackbrush are natural and not a grazing disclimax. Information is also made available showing those soil conditions which have the ability to produce plant communities dominated by grass with blackbrush a minor component.

Blackbrush (<u>Coleogyne</u> <u>ramosissima</u> Torr.)--An Important but Little Known Major Vegetation Type

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Blackbrush dominates probably the least studied major vegetation type in the coterminous United States, and is endemic to the Colorado River drainage. In Utah this species is a dominant on approximately 2 1/2 million acres. Blackbrush occupies an intermediate position between the northern (cold) deserts and the southern (hot) deserts, and has been classified as a paleoendemic which is a relictual endemic left by the extinction of its close relatives. Blackbrush and other monotypic and ditypic genera are also thought to be survivors of once-more-widespread groups and their present distribution represents a restriction in their ranges with time.

In southwestern Utah blackbrush is found on sandy loam soils exhibiting an A-C horizon sequence, and are underlain with a petrocalcic horizon. In eastern Utah blackbrush is found on the sands.

Growth and flowering occurs during the spring with some regrowth resulting from late summer storms. Summer dormancy, therefore, appears to be a result of soil moisture depletion rather than high temperature.

Winter and spring livestock grazing is the dominant use of this type, although blackbrush is generally considered to be a rather poor forage species. Perennial grasses are not found in much of this type and differing opinions have been expressed to explain this condition.

Burning has been used as a means of converting blackbrush stands to more desirable forage species. This has been successful when done in conjunction with reseeding, but the effects of fire are, at best, unpredictable.

Mature blackbrush develops a spinescent growth form and removal of this woody material should make the plants more desirable to grazing animals. Simulated brush beating removes this old growth and stimulates the production of basal shoots.

Germination, Survival, and Growth of Selected Browse Species in the Black Hills of South Dakota

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This paper reports on techniques developed and results obtained from a 10-year study conducted with selected browse species planted on burned and unburned ponderosa pine sites in the central Black Hills of South Dakota. The area is an important deer winter range and has experienced a long-term, continuing deterioration of important shrubs.

Objectives were to determine the best suited native and exotic browse species for planting on the two habitat types and the most effective method for their establishment.

Native shrubs selected for planting were: Chokecherry (*Prunus virginiana*), pin cherry (*P. pensylvanica*), common juniper (*Juniperus communis*), mountain-mahogany (*Cercocarpus montanus*), serviceberry (*Amelanchier alnifolia*), and inland ceanothos (*Ceanothos ovatus*). Exotic shrubs planted were bitterbrush (*Purshia tridentata*), silver buffaloberry (*Shepherdia argentea*), and silverberry (*Elaeagnus commutata*).

The planting design compared germination, survival and growth of shrub species for three planting years, two sites and three planting techniques. The planting techniques were 1) direct field seeding in fall, 2) transplanting potted seedlings in the spring and 3) spring planting of bare-rooted nursery stock. Various methods were used to break seed dormacy.

For ten years following initial planting, growth and survival of browse species planted on the burned site generally exceeded those on the pine site. Mortality for all shrub species was highest during the first two years on both sites.

Mountain-mahogany and bitterbrush grew better than other species planted by direct seeding. Chokecherry established by planting nursery stock did better than those fields seeded or planted as potted seedlings. Silverberry and silver buffaloberry grew best of the bare-rooted nursery stock. Serviceberry, common juniper, and inland ceanothos had poor success at both sites. Results of this 10-year study indicated shrubs can be re-established on depleted game ranges.

Environmental Gradient Analysis and its Application to the Distribution Patterns of Salt Desert Shrub Species

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Forty-seven study sites were located in the vegetational zonation patterns surrounding a salt desert playa near Goshen, Utah. Frequency and presence data were taken for all observed participating plant species. Salt, moisture and pH data were also obtained from each of the study sites. Environmental gradients were then established and species response curves to these gradients were determined. Salt and moisture gradients were shown to account for much of the variation observed in individual species distribution patterns.

Organic Fermentation Residues as a Nitrogen Source and Soil Amendment in Woody Plantings

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Massive amounts of high protein organic mycelial residues resulting from the production of citric acid by fermentation have been discarded until recent years. The Connecticut Arboretum tested the use of this by-product as a substitute N source and a moisture-holding soil amendment for the growth of trees and shrubs useful for roadside plantings, revegetation of gravel pits and rights of way. Three experimental treatments and a control were established. The mycelium residue was harrowed into the plowed surface at the rate of 40 wet tons per acre and 20 wet tons per acre plus 100 lb. of 5-10-10 fertilizer per acre. In mycelial-treated plots, growth was either normal or enhanced in the following shrub genera: *Cornus*, *Cotoneaster*, evergreen *Ilex* spp., *Juniperus* spp., *Ligustrum*, *Lonicera*, *Magnolia*, *Myrica*, *Prunus*, *Rhus*, *Rosa*. Some deciduous bare root material leafed out later in mycelium treated plots and showed signs of severe leaf burn and stunting which disappeared as the high ammonia N level in the soil declined and the nitrate level rose. This group included the trees *Cornus*, *Crataegus*, *Quercus*, and the shrubs *Alnus*, *Eleagnus*, *Ilex* spp., *Rhododendron*, *Sambucus*, *Symphoricarpos*, *Vaccinium* spp., and *Viburnum* spp. Severe stunting occurred in *Pinus* seedlings. Results indicate that mycelium residue incorporated into sandy loam soil at least six weeks in advance of planting can be a valuable fertilizer substitute and soil amendment in land reclamation.

Phenodynamics and Environmental Characteristics of Sagebrush-Grass Rangelands

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Phenodynamics are of primary importance when interrelated with vegetation production, environmental phenomena, and management of rangelands. However, very little detailed phenology, productivity, and environmental information is available for arid land species of the western United States.

Intensive phenological studies have been located on selected sagebrush-grass areas distributed throughout the western half of Wyoming. These areas express a broad ecological amplitude. Seventeen recognizable phenophases were devised for shrubs, forbs, and grasses. All flowering species in each study area were included in the study. Phenological data and environmental parameters (precipitation, maximum and minimum temperature, soil temperature, and percent soil moisture) were measured year-round at two-week intervals.

Variation in times and amounts of plant growth occurred within the same species, the same year, and the same location. Soil temperature is one of the primary driving factors in phenology. Significant changes in plant growth occurred with only a 0.5°C change in soil temperature. The relationship between soil moisture and phenology was less obvious. Seed dispersal occurred about the same time through two complete growth cycles; whereas initiation of growth and bloom times were quite variable. Other environmental phenomena which were important in driving and regulating plant growth were precipitation from fall through spring, soil moisture at various depths, and maximum-minimum air temperatures.

Multiple regression and step-wise selection analysis procedures were used to substantiate or reject relationships observed from interpretation of field data, which included phenological information and fifteen environmental variables.

Ecology of the Sagebrush-Community as Influenced by Some Natural and Man-Caused Perturbations

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Much has been written about how lush grasslands found in foothills and valleys at the time of settlement were transformed into areas dominated by shrubs, mainly sagebrush, by overgrazing. For example, early settlers in the south end of Rush Valley, Utah, reported that at one time it was possible to cut native grass hay across the entire valley and that upwards of 10,000 head of cattle and horses grazed there year-round. By 1900, when it was considered that the area had possibilities for dry land farming, the plows were turning over sagebrush for the most part.

When dry farming failed during the drought years of the early 1930's, the Federal Government purchased the land and reseeded thousands of acres to crested wheatgrass. This provided opportunity for ecological studies on different types of land as follows: 1) abandoned farm land seeded to crested wheatgrass, 2) abandoned farm land not seeded to grass, and 3) land that had been overgrazed but not plowed nor seeded.

At present, the area abandoned from dry farming some 50 years ago but not seeded supports almost a pure stand of big sagebrush having essentially no herbaceous understory and no value for grazing of cattle. In contrast, an adjacent area once depleted by overgrazing but not plowed now supports an almost pure stand of herbaceous species where sagebrush control measures have been applied. The latter area will support grazing at a level of approximately 2 1/2 acres per cow month. Between these extremes are variations in the amounts of sagebrush and grass caused by such things as fire, herbicides, grazing by different classes of livestock, etc., all of which will be discussed.

Evolutionary Development of the Artemisia tridentata Taxa

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This paper presents evidences concerning the origin of the present taxa included under the big sagebrush group (Artemisia tridentata). The original ancestor is proposed to be a mountain taxon, Artemisia tridentata subsp. vaseyana, not the basin taxon A. tridentata subsp. tridentat as previously reported. It is proposed that subsp. tridentata is an offshoot from subsp. vaseyana and that subsp. wyomingensis developed as a hybrid between subsp. tridentata and A. nova. Form spiciformis is proposed to be an autotetraploid variant of subsp. vaseyana and a proposal is put forward to raise it to a subspecies level. An Artemisia variant from higher elevations in the Wasatch Mountains of Northeastern Utah, Southeastern Idaho and Western Wyoming is apparently often erroneously referred to as A. rothrockii. Origin of this variant (A. cana subsp. viscidula X form spiciformis) as well as its morphological characteristics suggest it should be influded as a subspecies of the big sagebrush group. A newly recognized big sagebrush variant (type "X") is proposed to be a product of recent crossing of subsp. vaseyana and subsp. tridentata and should receive subspecies status. Evidence supporting proposals in this paper include ecological, morphological, chemical, cytological and phenological data.

Genetic Studies in Section Tridentatae of Artemisia

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Big sagebrush (Artemisia tridentata) and its relatives comprise the section Tridentatae of Artemisia. This group of plants is endemic to western North America where they are conspicuous members of the shrub community. They are important browse plants both for big game and domestic animals and provide habitat for many smaller animals as well as serving in other functions.

We have begun investigations on the Tridentatae to more clearly understand their intrarelationships so they might advantageously be utilized. Our research is centered on the subspecies of A. tridentata (tridentata, vaseyana, and wyomingensis). Our efforts are broadly divisible into 1) chromosome studies, 2) hybridization studies, and 3) chemical and numerical studies.

The Tridentatae form a polyploid complex based on $x=9$ ranging from diploid, $n=9$, to octoploid, $n=36$. Evidence so far available from meiotic chromosome pairing and mitotic karyotypes indicates it is an autopolyploid complex; i.e., one genome in single or multiple sets is present in each taxa.

The Tridentatae have only perfect disk flowers. The single exception is A. bigelovii which also has pistillate ray flowers. Self- and wind-pollination occur. Bees and other insects often collect Artemisia pollen and presumably act as pollinators. Some putative natural hybrids have been discovered. Two years artificial hybridization data have shown that, despite their self-fertility, semicontrolled cross pollination is possible for these shrubs.

Numerical and chemical studies confirm morphological taxa--though there are some populations which do not conveniently fit described taxa.

with deeper soils. Artemisia tridentata wyomingensis is lacking in the northern Great Basin and high central Nevada ranges. It prefers the driest, warmest kinds of woodland sites in the more southerly portions of the Great Basin. Artemisia nova is generally lacking in the more arid portions of the Great Basin in both western Nevada and western Utah but occupies sites of intermediate favorableness elsewhere.

Sampling Big Sagebrush for Phytomass

D. W. Uresk, R. O. Gilbert and W. H. Rickard

Battelle Laboratories, Richland, Washington

Big sagebrush, Artemisia tridentata, was subjected to a double sampling procedure to obtain reliable phytomass estimates for leaves, infloresence heads, livewood, deadwood, various combinations of the preceeding, plus total phytomass. Data were collected on the Energy Research and Development Administration's Hanford Reservation, Benton County, Washington.

Dimension measurements were made on individual shrubs which were selected at random within a 300 x 300 meter area for the following: 1) canopy diameter (length), 2) canopy diameter (width), and 3) shrub height. A random subset of these shrubs were then harvested at ground level, separated by categories and oven dry weights obtained.

The study area has an estimated 2,342 shrubs/ha of which 1,577 and 765 are live and dead, respectively. Average length of live shrubs was 71±1 cm with a width of 48±1 cm. Average height was 49±1 cm. Volume

(length x width x height) was used as the independent variable in the double sampling scheme to estimate phytomass for all categories except for flowers and seeds and miscellaneous items. The independent variable length was used for these categories.

The correlation coefficients (r) between the independent variable and the various phytomass categories ranged from a low of 0.67 to a high of 0.93. Livewood made up approximately 62% of the total phytomass of sagebrush. Deadwood accounted for 11% while leaves and floral parts comprised 14 and 8% of the total, respectively. Double sampling for sagebrush phytomass was an effective technique in reducing the variance of phytomass estimates. Estimated reductions were obtained for the various categories under optimum allocation.

Distribution and Indicator Values of Artemisia Within the Juniper-Pinyon Woodlands of the Great Basin

Neil E. West, Kenneth H. Rea, Robin J. Tausch[1] and Paul T. Tueller[2]

[1]Professor, Research Technician, and Graduate Research Assistant respectively, Department of Range Science, Utah State University, Logan, Utah. [2]Professor, Renewable Resources Center, University of Nevada, Reno, Nevada.

Sagebrushes (woody Artemisia spp.) are the most common associates of the juniper/pinyon-dominated woodlands of the Great Basin. Understanding of the distribution and indicator significance of the various Artemisia species is therefore of major importance in judging site conditions in this cover type. Data collected at 374 juniper-pinyon woodland

sites on 65 mountain ranges scattered across the entire Great Basin have yielded an understanding of the areal distribution and environmental relationships for five *Artemisia* taxa. These sagebrushes rarely occur together. The separations observed were poorly related to geological substrates and land forms and only secondarily to soils. It is probable, however, that the broad distribution is primarily related to climatic patterns. With few climatic stations available, we must infer from slope, exposure and elevation what these relationships may be. Only the higher and larger mountains and thus wettest and coolest of pigmy conifer woodlands in the central and southern Great Basin have *A. tridentata vaseyana*. To the north and west *A. tridentata vaseyana* increases in dominance until at the northeastern limits it is the only species present. *Artemisia arbuscula* is widely scattered on cold, dry sites with shallow soils on the higher mountains all across the Great Basin. *Artemisia tridentata tridentata* is lacking in the woodlands of the southern Great Basin. Where this taxon occurs on the northern ranges, it is on the warmer, wetter sites with deeper soils. *Artemisia tridentata wyomingensis* is lacking in the northern Great Basin and high central Nevada ranges. It prefers the driest, warmest kinds of woodland sites in the more southerly portions of the Great Basin. *Artemisia nova* is generally lacking in the more arid portions of the Great Basin in both western Nevada and western Utah but occupies sites of intermediate favorableness elsewhere.

Section III -- Dedication of the U.S. Forest Service Shrub Sciences Laboratory, Program

THE FOREST SERVICE

U.S. DEPARTMENT OF AGRICULTURE

cordially invites you

to attend the dedication of the

SHRUB SCIENCES LABORATORY

Provo, Utah

A new research facility of the Intermountain Forest and Range Experiment Station on the campus of and in cooperation with Brigham Young University

PROGRAM

Thursday, November 6, 1975 - 2:00 to 3:00 p.m.

Varsity Theatre, Wilkinson Center

Brigham Young University

MASTER OF CEREMONIES	Roger R. Bay, Director, Intermountain Forest and Range Experiment Station
INVOCATION	Max V. Wallentine, Salem Stake Presidency, Church of Jesus Christ of Latter-day Saints
WELCOME	Dallin H. Oaks, President, Brigham Young University
RECOGNITION OF GUESTS	Roger R. Bay, Director, Intermountain Forest and Range Experiment Station
REMARKS	Bud Phelps, Director, Utah Division of Wildlife Resources
	Robert J. Smith, Asst. Vice President Brigham Young University
	Doyle J. Matthews, Dean, College of Agriculture, Utah State University
DEDICATION ADDRESS	Warren T. Doolittle, Associate Deputy Chief, Forest Service, U.S. Department of Agriculture

Official Opening and Tour of Laboratory - 3:00 to 4:30 p.m.
(735 North 500 East)